

A TAXONOMIC REVISION
OF THE GENUS XANTHOCNEMIS (ODONATA: COENAGRIONIDAE)
AND
AN INVESTIGATION OF THE LARVAL BEHAVIOUR OF
XANTHOCNEMIS ZEALANDICA

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ABSTRACT

The genus Xanthocnemis (Odonata: Coenagrionidae) is endemic to New Zealand and includes 4 described species. Of these X. tuanuii is confined to the Chatham Islands, X. sobrina in Northland forests and X. sinclairi is described for the first time from Whitcombe Pass in the headwaters of the Rakaia River. Xanthocnemis zealandica (McLachlan) is the commonest and most widely distributed species, occurring on the 3 main islands of New Zealand in many still and some running water habitats. In the present study, larval behaviour was examined extensively in laboratory aquaria with particular emphasis on interactions with conspecifics and the use of defended, territorial sites. Field studies were used to complement laboratory work on feeding.

X. zealandica larvae have an extensive repertoire of agonistic displays 25 of which are identified and described. All are associated with site defence. Larvae adopt a sedentary behaviour pattern from the earliest free living stage and many displays are well developed by instar 5. Late instar larvae select particular types of sites on stems with a preference for those of 4-7 mm diameter observed in experimental work. They often remain on a particular site for many weeks. This was consistent with what was known of their behaviour in the field.

It was found that the perches occupied probably served the larvae primarily as refuges from predators rather than as 'fishing sites'. Behaviour on sites was insensitive to feeding regimes, i.e. different prey type and density. The sites were effective refuges against some invertebrate predators including larval and adult Dytiscidae. It is considered that the 'sit and wait' tactics of X. zealandica are mainly associated with predator avoidance.

The sedentary and cryptic behaviour of X. zealandica made experimental investigation of the predatory behaviour of larvae impracticable. However, the opportunity was taken to examine the varied predatory behaviour of Hemianax papuensis (Aeshnidae) which was more amenable to study. This demonstrated unequivocally the presence of predatory versatility in odonate larvae.

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INTRODUCTION

The view of the physicist Fremlin (1979), that insects can be regarded as simple automata, represents a fair summary of conventional wisdom. For reasons which are obscure, recent evolutionary advances have been slow in penetrating entomological thought in general (Evans 1985), and the study of insect behaviour in particular (Thornhill & Alcock 1983).

There has been a failure to seek (and consequently a failure to find) behavioural versatility in insects. Vertebrate ecologists have long recognised the importance of flexible behaviour in shaping the ecology of species (e.g. Wilson 1975) but this viewpoint has, with some notable exceptions, failed to carry over to studies of insects. The adaptive benefits of behavioural plasticity and the extremely high rates of evolution achievable with behavioural characters have been emphasised by Lorenz (1967), Pyke (1984) and others. The view of insect behaviour has, in contrast, tended to follow Davis (1974) 'the extreme stereotypy of behavior of insects leaves little opportunity for behavioral interpretation' (see Curio 1976). With few exceptions the behavioural components of insect ecology have been glossed over. This conceptual failing may be due to the tendency for ethologists and behavioural ecologists to work in the main with vertebrates while insect behaviour has largely been the domain of neurophysiologists with limited input from ecologists.

There are practical difficulties in working with insects: they are small, adults tend to be mobile, short lived and largely occupied in stereotyped sexual behaviours while larvae are often cryptic and restricted to certain (often inaccessible) microhabitats. In the laboratory there are problems with confinement, and the maintenance of suitable microhabitats as many species are sensitive to slight changes in

temperature or humidity. The use of long lived, aquatic insect larvae circumvents many of these practical problems.

Lawton et al (1980) suggested that damselfly larvae in general are 'sit and wait' predators which would forage optimally, selecting the best possible 'fishing sites', even though, as they demonstrated, death from starvation was not a significant threat in the field. They noted that 'The problems of how damselfly larvae select hunting sites, what makes them change sites, and the risks which they expose themselves to when and if they do require further investigation'.

Whereas the ecological requirements of adult dragonflies are broadly similar and, except for mating and oviposition sites, largely unspecialised (Corbet 1962), larval Odonata often display narrow habitat preferences. Corbet (1962) concluded that adaptive radiation in larval functional morphology 'has presumably been necessitated by interspecific competition for space and food in the relatively confined aquatic habitat', a contention supported by Gilpin (1974).

Within the Odonata, the Coenagrionidae are a remarkably successful family and are dominant amongst present-day Zygoptera (Tillyard 1926, Fraser 1957). Considerable speciation and adaptive radiation has occurred with species occupying a broad spectrum of (larval) habitats. An extreme example of this is found in the genus Megalagrion (Coenagrionidae: Pseudagrioninae) from Hawaii, where the larval habitats of species range from free flowing streams to terrestrial leaf litter. Larval Coenagrionidae are a common component of the littoral fauna of most temperate and tropical freshwaters and in many systems they are the numerically dominant invertebrate carnivores (e.g. Chutter 1961, Macan 1964, Petr 1968, Lawton 1970a, Pearlstone 1973, Johannsson 1978). Well represented genera include Argia (150 sp.), Coenagrion (88 sp.), Enallagma (80 sp.), Ischnura (78 sp.) and Pseudagrion (about 200 sp.) (Davies 1981).

Xanthocnemis, the endemic New Zealand genus in the Coenagrionidae, comprises four close sibling species. Larvae of the widespread species X. zealandica (McLachlan) are common in the littoral zone of most lakes and ponds throughout the country and also in streams and rivers (Rowe in press). Larvae are usually semivoltine (Deacon 1979) but may mature in one (Crumpton 1979, Rowe in press) or three years (Deacon 1979). Seasonal regulation in the population used to supply animals for experimental work in this study is covered in Deacon (1979) and the general biology of the species is outlined by Rowe (in press). The larvae are territorial, thigmotactic, 'sit and wait', ambush predators. Previous studies of the biology of X. zealandica larvae were undertaken by Scott (1971), Mylechreest (1978), Crumpton (1979), Deacon (1979), Rowe 1978a, 1980) and Stark (1981). During the course of this study Dowdle (1981) examined the diet of X. zealandica larvae at my main collection site as part of a wider study of interactions between arthropod predators.

In this study I considered parameters influencing site selection, the duration of site occupancy and behaviours involved in intraspecific site defence in final instar larvae. Changes in site occupancy during larval development and the development of intraspecific agonistic displays were also investigated. A limited comparative study was made of site usage by Ischnura aurora (Brauer) (Coenagrionidae) and Austrolestes colenisonis (White) (Lestidae) and the agonistic displays of these species were documented.

Feeding rates were examined in the field for comparison with the laboratory studies. Attempts to investigate the predatory behaviour of X. zealandica in detail were frustrated by the cryptic behaviour of the species. An opportunity to examine the larval behaviour of Hemianax papuensis (Burmeister) was used to demonstrate unequivocally the existence of predatory versatility in odonate larvae.

Prey composition and availability appeared to have little effect on site selection or site occupation by X. zealandica larvae and alternative adaptive aspects of site use were investigated. The perches selected were shown to be effective 'antipredation' sites and X. zealandica larvae proved to have antipredation behaviours matched to the sites used.

'Sit and wait' predators per se provide an important test for theories of foraging behaviour. Their success in terms of both species and individual numbers, especially among arthropods, and their manifest failure to forage make them an important challenge to any general theory of predatory behaviour. Recent theories of predatory behaviour have been largely the products of schools studying small birds and small mammals; generalisations based on familiarity with these specialised taxa may have little bearing on broader evolutionary questions. The near absence of data on individual predatory behaviours of arthropods have seriously hampered the mounting of challenges to the emerging theories from what represent the vast majority of life forms.

In the scheme of Hassell & Southwood (1978), 'sit and wait' damselfly larvae present a particularly clearcut example of random foragers. Within the habitat selected by the ovipositing female, larvae choose 'patches' according to the perches they occupy. Within their patch, larvae are 'random foragers' insofar as prey arrival in the 'attack volume' surrounding the perch is stochastic and independent of any 'searching' by the larva.

As insects form a large proportion of life forms and as many insect predators use 'sit and wait' predatory behaviours; an understanding of the ramifications of these strategies would be useful when considering broader questions in biology. So far as I am aware there have been no long term studies of insect 'sit and wait' predators.

While in a number of insects long, complex, behaviour sequences triggered by a single cue have been documented; it would be misleading to regard insects as automatons. Such sequences occur in situations where selection pressures for simple responses might be expected, and similar automaton like behaviour patterns are known in many phyla including vertebrates. Under circumstances where behavioural versatility is adaptive insects may display a considerable flexibility in their responses. Insects are not uniform and noticeable individual variation in behaviour occurs. As natural selection acts at the level of the individual it is important to consider the potential consequences of these individual variations.

Organisation of the thesis.

The thesis is divided into six sections dealing with: taxonomy of the genus Xanthocnemis; agonistic displays used during site defence; aspects of the predatory activity of dragonfly larvae; use of space by X. zealandica larvae and the value of the territorial sites occupied. Each section is headed by a brief statement placing the section in context and comprises one or more chapters. There are four appendices: the first describes some mathematical techniques used; the second examines predatory versatility in Hemianax papuensis (Burmeister) (Anisoptera: Aeshnidae); the third details the effect of perch diameter on foraging and predator avoidance success and the fourth contains data on site occupation.

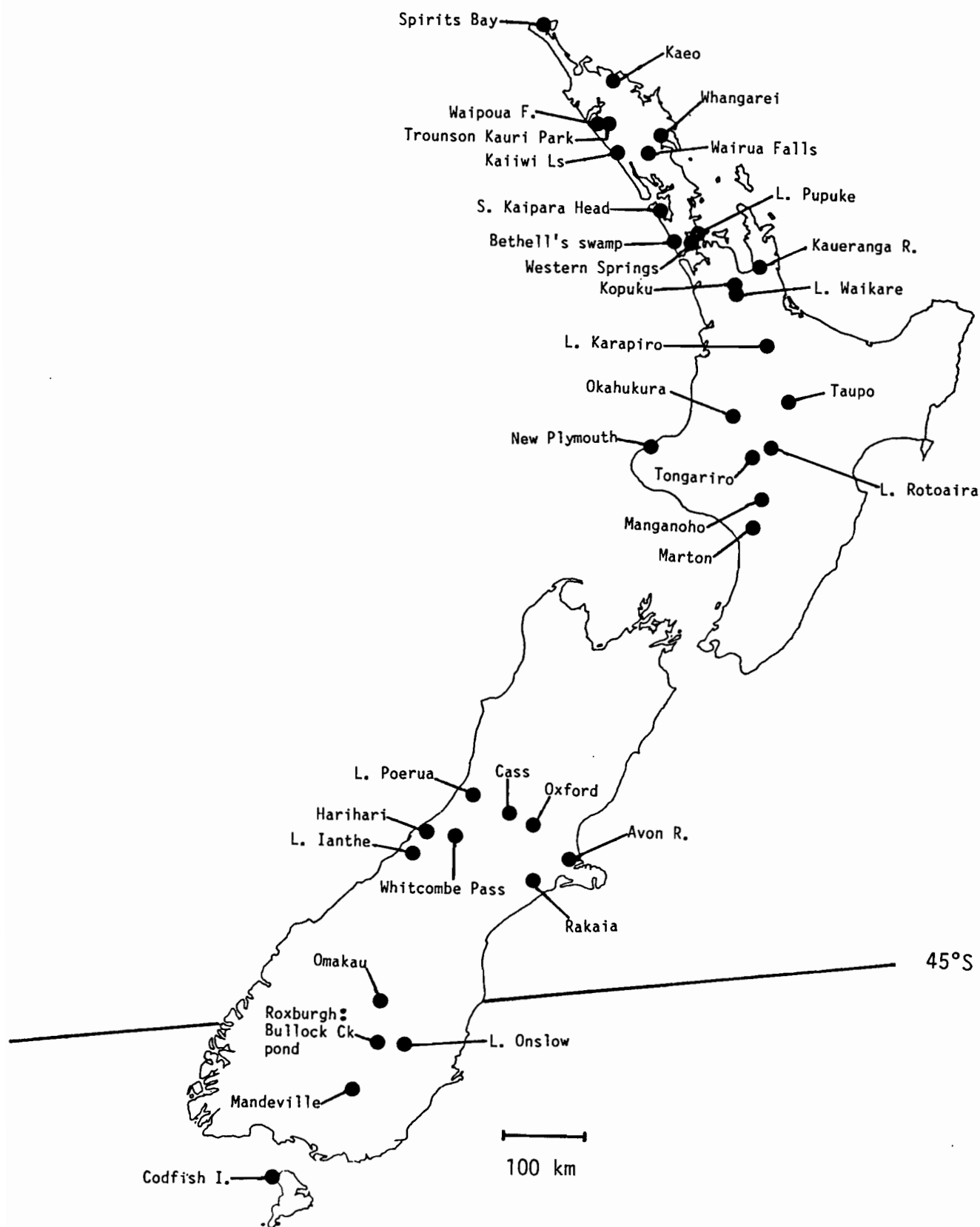


Fig. 1. Map of New Zealand indicating the position of localities cited in the text.

Section 1: Taxonomy

At the time this study began only one species of Xanthocnemis, X. zealandica (McLachlan 1873), was recognised in the literature. However, two knowledgeable commentators regarded this species as being 'suspiciously variable' (P.S. Corbet, J.A.L. Watson pers. comm.). An additional species, X. sobrina (McLachlan 1873), had been recognised by J.S. Armstrong and myself. Kimmins (1970) also recognised this species, but checklists (e.g. Wise 1965, 1977) relegated it to a junior synonym of X. zealandica. As behavioural studies are highly susceptible to the confounding effects of interspecific differences if these are not recognised and allowed for, it was imperative that the taxonomy of the genus Xanthocnemis was clarified.

Scanning electron micrographs of the male anal appendages showed clearly that the species X. zealandica and X. sobrina were distinct. An expedition to the Chatham Islands uncovered a previously unsuspected species, X. tuanuii Rowe 1981, and a collecting trip to the headwaters of the Rakaia R. in the South Island allowed me to collect more specimens of yet another new species.

Attempts to gather material to permit comparative studies of larval displays and predatory behaviours in these close sibling species were largely unsuccessful. No larvae of X. sobrina or the Rakaia species were transported successfully to Christchurch. Ova from Chatham Island and from the headwaters of the Rakaia R. failed to hatch on being returned to the laboratory. This was almost certainly due to temperature changes in transit (e.g. the Rakaia material was backpacked down the river bed for two days in a scorching nor'wester). Ova of X. sobrina were obtained in Auckland and Christchurch from animals collected in the Waipoua forest. The low temperature required by the ova and early instar larvae of this species was not anticipated and most died. Two animals were raised to the 8th instar under what were probably far from ideal

conditions. With the equipment and techniques I was using then this was still too early to study intraspecific agonistic behaviours.

All stocks used in behavioural investigations came from sites where X. zealandica was the only species found. Parentage of all ova used was determined by collecting and examining the copulating male. The main source of larvae was a pond at the Cass Biological Field Station (43°02'S 171°46'E) (Remus pond of Dowdle 1981) with supplementary stocks being taken from Typha orientalis beds at L. Sarah (43°03'S 171°47'E). At various times larvae from a number of other sites were examined – Kaiwi Ls (35°48'S 173°39'E), Bethel's swamp (36°54'S 174°27'E), L. Pupuke (36°47'S 174°46'E), Dillmanstown (42°39'S 171°12'E), Belfast (43°25'S 172°39'E), R. Avon (43°31'S 172°35'E) and Roxburgh (45°29'S 169°19'E). No differences were observed in the territorial display behaviours of X. zealandica larvae from different localities. Second instar X. sobrina larvae, unlike those of X. zealandica, did not localise on perches in the laboratory, but this may have been a consequence of thermal stress.

CHAPTER 1

A revision of the endemic New Zealand genus Xanthocnemis Tillyard
with the description of a fourth, subalpine, species.

INTRODUCTION

McLachlan (1873) erected the species Telebasis zealandica and T. sobrina for two coenagrionid dragonflies from New Zealand. The specimens on which the species were based probably included those collected by Andrew Sinclair in the Bay of Islands in 1840 (on the basis of White 1843, McLachlan 1873, Brooks pers. comm). T. sobrina was based on a single immature male specimen. Selys (1876) transferred both species to the genus Xanthagrion using the trivial form zealandicum for zealandica (this error may have been McLachlan's as his 1873 description was footnoted as a Selys' manuscript name); and erected a further species X. antipodum based on a single female specimen of an unusually small size.

McLachlan (1894) challenged the validity of antipodum, but on examining a further series of specimens emphasised his confidence in the species sobrina stating 'Colonial entomologists will do well in carefully studying these small Dragon-flies'. Hutton (1898) identified specimens from Chatham Island as Xanthagrion sobrinum but commented on 'differences' they showed from mainland forms. The following year he listed X. zealandicum, sobrinum, and antipodum as occurring in New Zealand (Hutton 1899). This listing was repeated by Hudson (1904).

Tillyard (1913a) erected the genus Xanthocnemis to contain McLachlan's Telebasis zealandica (cited as Xanthagrion zealandicum Selys 1876), and synonymised sobrina and antipodum with this species.

Tillyard's revision was rather careless and it is apparent from the text that he did not refer to the types when making these synonymies. Tillyard referred to 'Specimens..... received from Chatham Island, are exceptionally fine, and the largest of the whole series'. Generally, Chatham Island Xanthocnemis (X. tuanuii Rowe 1981) are larger than X. zealandica from the main islands, but nonetheless they are markedly smaller than McLachlan's sobrina. The anal appendages figured bear little resemblance to any New Zealand species, but might be X. tuanuii. It would appear that Tillyard accepted specimens forwarded from some New Zealand collector as being properly determined material on which to base his revision. Later, after working in New Zealand, Tillyard reversed his position (Tillyard 1926) and stated that four species of Coenagrionidae occurred in New Zealand, the only common one being 'X. zealandica Sel.'. He also noted the first record of Ischnura aurora.

Tillyard's 1913 opinion remained entrenched in New Zealand entomological circles and his 1926 recantation was ignored (e.g. Wise 1965, 1977, Penniket 1966, Dumbleton 1970). Nevertheless, the late Dr J.S. Armstrong was strongly of the opinion that the 'variation' in X. zealandica masked the existence of further species and that X. sobrina was a valid species. At his suggestion I began work on this group.

Dr M.A. Lieftinck examined Selys' X. antipodum type in the Brussels Museum and (pers. comm. in lit. to J.S. Armstrong (25 Jan. 1965)) expressed the opinion that it was merely a rather small X. zealandica, and not outside the size range he had himself observed while touring New Zealand. Mr D.E. Kimmins (British Museum (Natural History)) examined McLachlan's types in 1965 and expressed the strong opinion that they represented distinct species - an opinion followed in Kimmins (1970). Kimmins' drawings of the appendages of the type sobrina corresponded with the appearance of specimens J.S. Armstrong had believed were that species. In 1979, Mr S. Brooks (British Museum (Natural

History)) prepared further drawings of the McLachlan type material which confirmed that Armstrong's concept of X. sobrina was correct.

In an attempt to discover whether there was any pattern to the large, apparently intraspecific, variability of X. zealandica I examined several hundred specimens from a wide variety of habitats and locations. During this work I received, from Margot and Peter Syms*, alpine specimens that obviously belonged to a further species. I was later able to visit the locality where they had collected and acquired sufficient specimens to complete a description.

Genus Xanthocnemis Tillyard 1913

Diagnosis: Pseudagrionine genus with Ac lying midway between antenodals. 1A leaving posterior wing margin just basally of Ac in forewing and at Ac in hindwing. Inferior appendages of male much longer than superiors. This diagnosis is inadequate as in many specimens of X. sinclairi 1A leaves the posterior wing margin basally of Ac in both fore and hindwings and Ac is basal of the midpoint of the antenodals.

Below the family level classification is uncertain within the Coenagrionidae (Fraser 1957, Davies 1981). The subfamily system in common use is that of Fraser (1957), based largely on the level of petiolation of the wing; this character may be subject to selection pressures, producing convergence that could, mistakenly, be interpreted as synapomorphies. Tillyard (1913a) placed Xanthocnemis in what is now the subfamily Pseudagrioninae but, on the basis of details of forewing venation (1A leaving the margin basal to Ac), considered that it was very close to the Coenagrioninae. The frequent occurrence of 1A leaving the margin basal to Ac in both wings of X. sinclairi casts doubt on the value of this character in higher taxonomy. Xanthocnemis is distinct

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from 'mainstream' coenagrionine and pseudagrionine species in the marked extension of the vein CuP, which reaches the wing margin approximately at the level of the pterostigma; Jensen (1980) established that the karyotype of X. zealandica differed from that recorded in any other pseudagrionine.

Contrived classifications erected for curatorial convenience and based on unstable characters will obscure phylogenetic relationships; by 'compartmentalising' taxa under consideration and influencing deductive processes such schemes actively hinder the discovery of more appropriate classifications. For this reason Fraser's (1957) subfamily classification of the Coenagrionidae requires serious re-evaluation.

The recent discovery of fossil Coenagrionidae from the early Cretaceous (Jarzembowski 1984) pushed the known age of the family back some 80MY (Carpenter pers. comm.) and it is conceivable that Xanthocnemis represents a Gondwanan element in New Zealand's fauna. Should this be so, then the phylogenetically closest species would be expected to occur in Australia or South America. The present day Australian Coenagrionidae are dominated by a northern element (Watson 1981). The only endemic Australian genera are the monotypic Xanthagrion and Caliagrion (Coenagrionidae: Pseudagrioninae). Xanthocnemis was formerly included in Xanthagrion (Selys 1876) and Caliagrion billinghami (Martin) resembles Xanthocnemis in having a strong CuP extending to the area below the pterostigma (J.A.L. Watson pers. comm.).

I would surmise that Xanthocnemis is allied to an older Australian coenagrionid fauna which existed prior to the Pleistocene and that this fauna largely disappeared during repeated glacial advances because its members were, in general, unable to penetrate into the new temperate areas against already established northern coenagrionids. The restriction of C. billinghami to south eastern Australia (Tillyard 1926, Watson 1974) and the occurrence of a distinct archaic southern

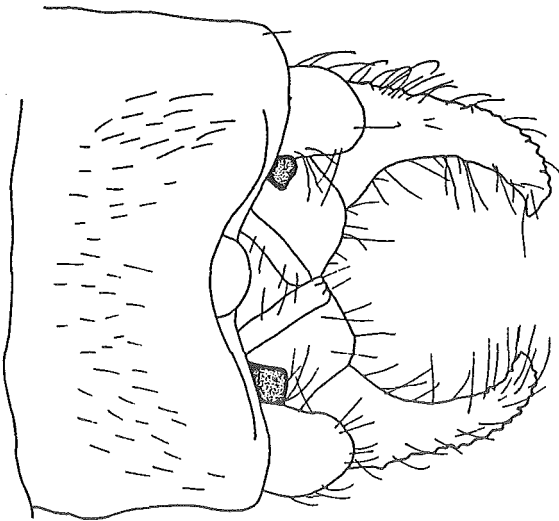
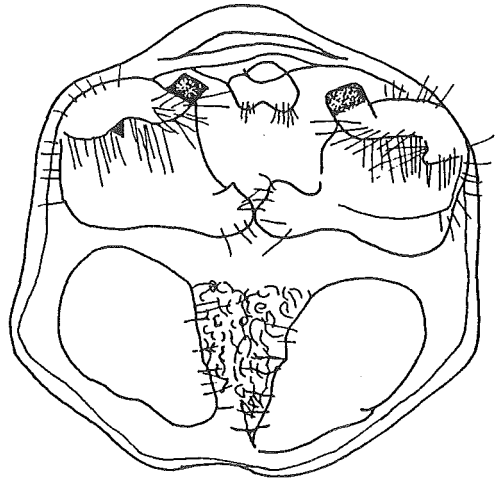
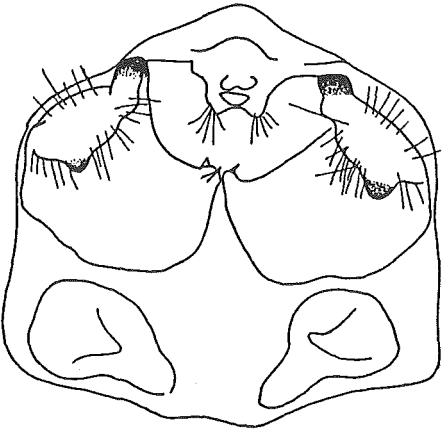
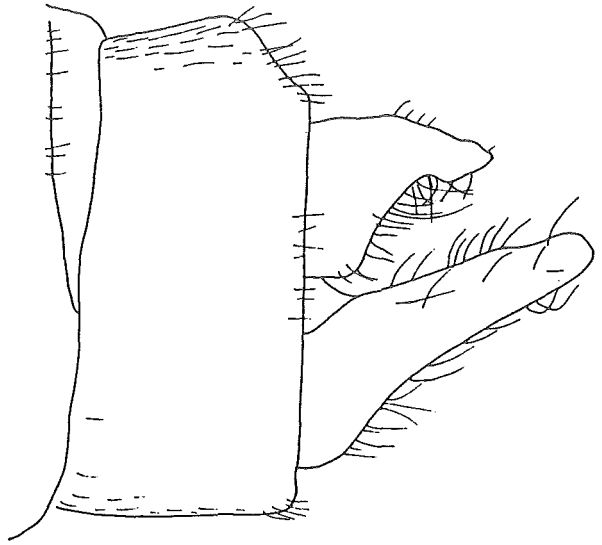
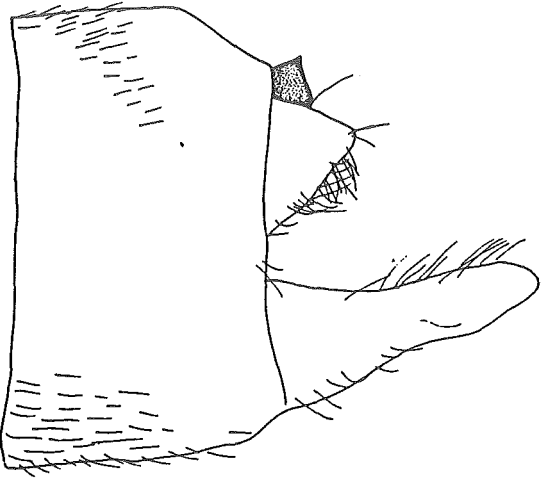
fauna within the Australian Odonata (e.g. Hemiphlebiidae, Aeshnidae, Corduliidae) (Watson 1981) is consistent with the earlier existence of an older, lost southern temperate coenagrionid/pseudagrionine fauna.

THE TAXA

The most reliable method for distinguishing the sibling Xanthocnemis species is the shape of the male superior appendage. Mating isolation in coenagrionid dragonflies was examined in some detail by Robertson & Paterson (1982) who showed that the shape of the male superior appendage was the main factor preventing interspecific copulation. This is compatible with the very heavy reliance placed on these organs by traditional taxonomists. As often occurs in the Coenagrionidae, females offer few diagnostic features and are most reliably determined by association with the males. There are differences in colour pattern between the heterochrome morphs (the female colour pattern dissimilar from that of the male) of at least three of the species. Within those species where it is known to occur, the androchrome morph (the female colour pattern similar to that of the male) varies widely in colour pattern. No attempt has been made to separate androchrome females. There are significant variations in the frequency of androchrome morph females among the species. Some differences are known between final instar larvae, but the reliability of the larval key requires verification.

Brooks' figures of the anal appendages of the types of X. zealandica and X. sobrina are reproduced in Fig. 2. SEM views of the anal appendages of X. zealandica from specimens collected in a variety of habitats throughout the geographical range are shown in Fig. 3 and SEM views of the remaining three species in Fig. 4.

Fig. 2. Anal appendages of the types of X. zealandica (left) and X. sobrina (right). Top - lateral view, middle - caudal view, bottom - dorsal view. (from originals by S. Brooks (BM(NH))).



1mm

Fig. 3. SEM views of the anal appendages of male X. zealandica
from a range of sites and habitats. Left to right:
Top to bottom: lateral, caudal, caudal detail
and dorsal views.
(scale bars = 0.5mm)

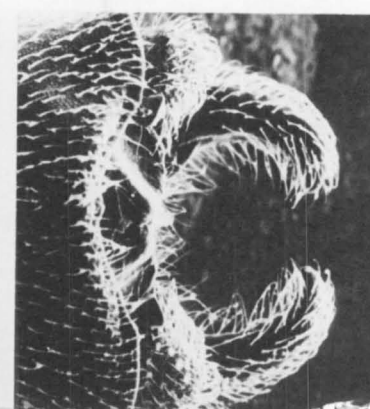
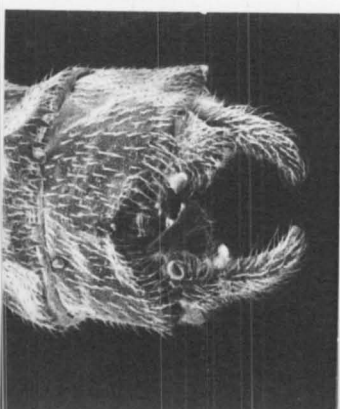
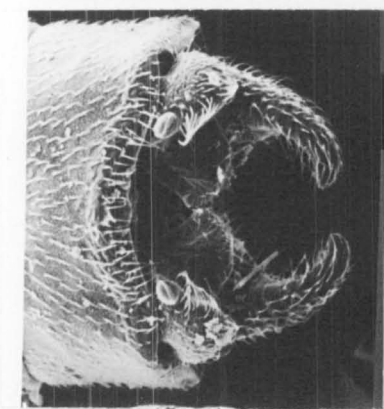
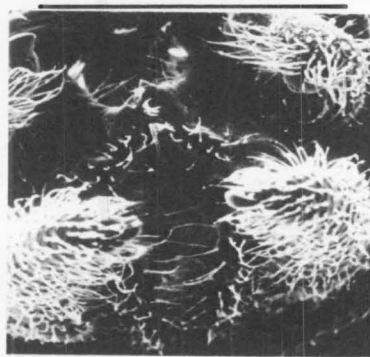
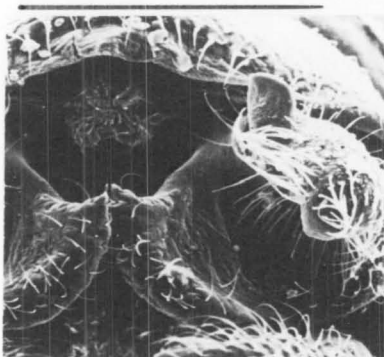
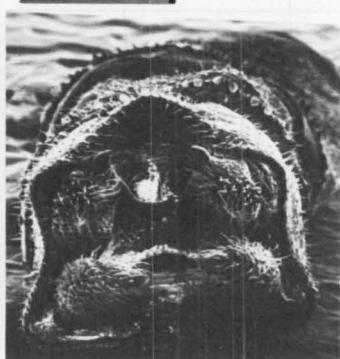
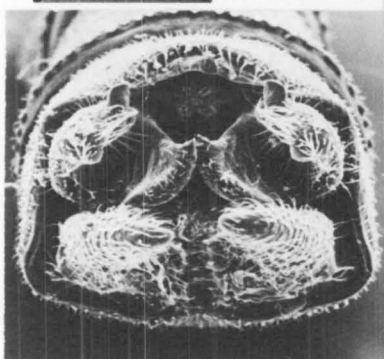
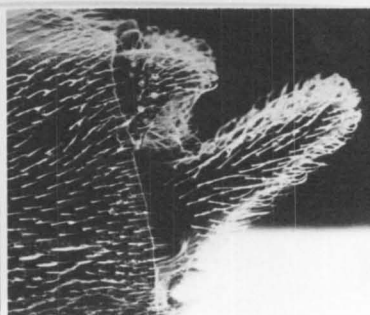
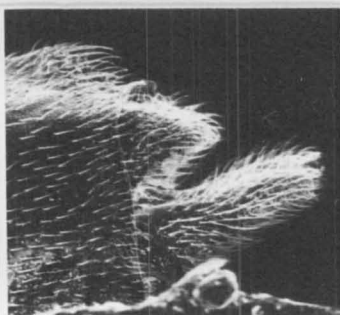
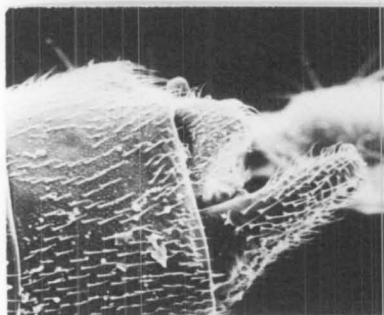
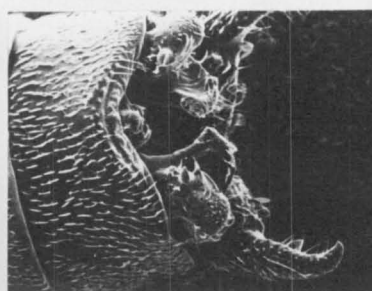
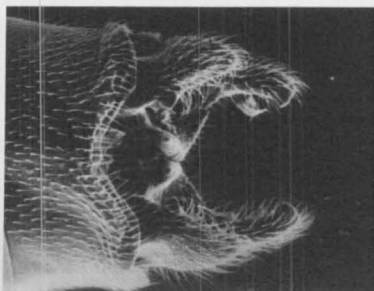
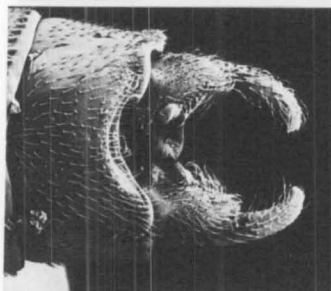
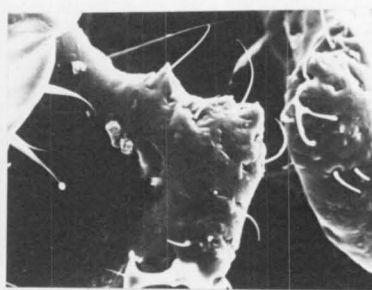
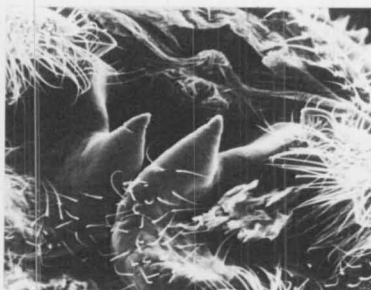
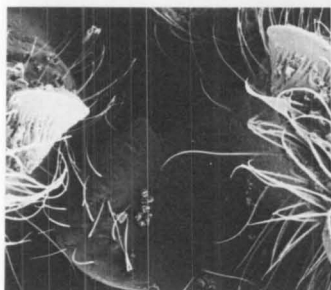
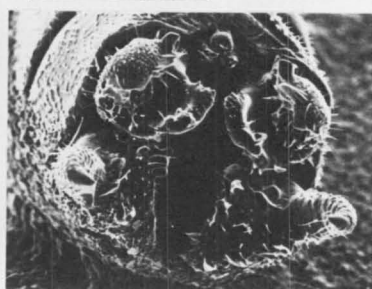
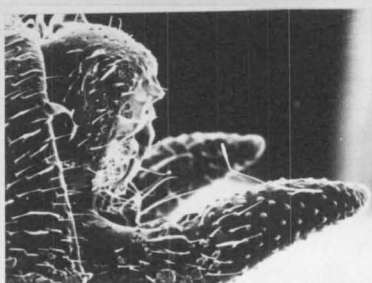
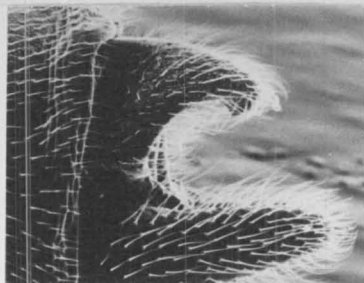
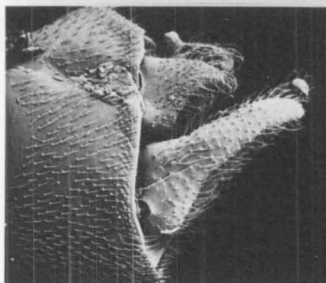


Fig. 4. SEM views of the anal appendages of (left to right):
X. sobrina (Waipoua F.), X. tuanuii (type locality),
X. sinclairi (type locality). Top to bottom: lateral,
caudal, caudal detail and dorsal views.
(scale bars = 0.5mm)



KEY TO THE MALES OF Xanthocnemis

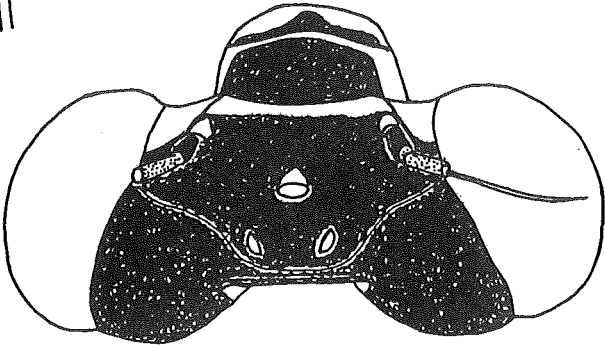
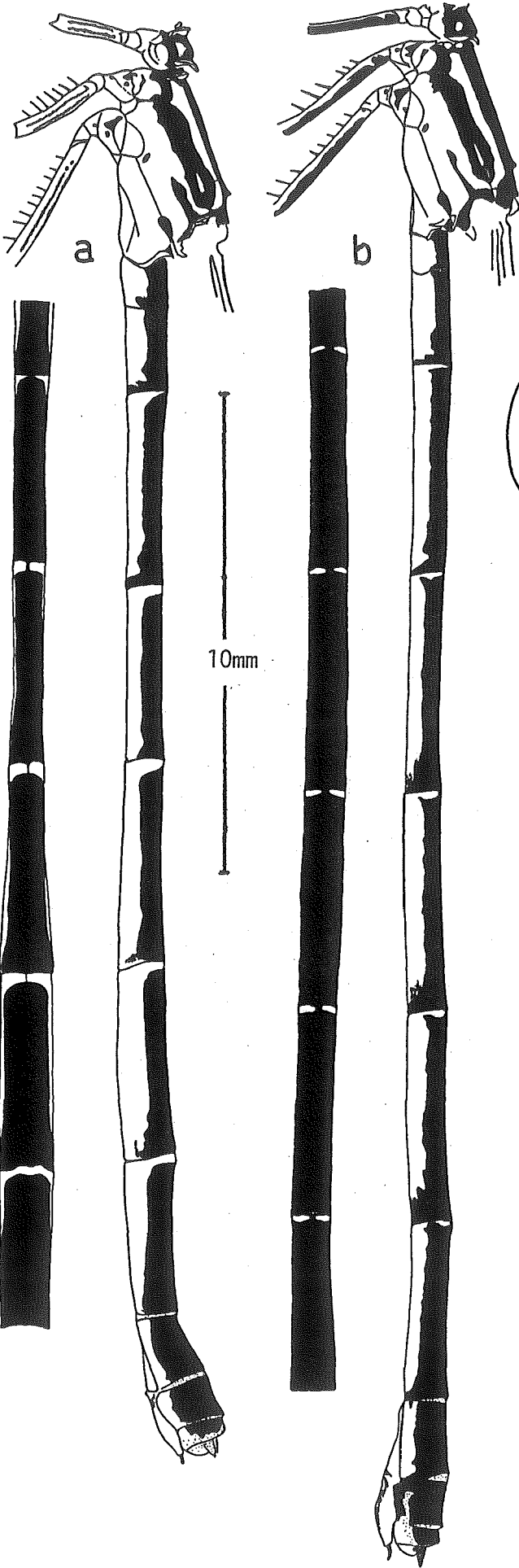
- 1 Lower lobe of superior appendage with rounded tip and sharp pointed, unsclerotised sub apical spinesobrina
 Lower lobe of superior appendage drawn into a strongly pointed tip...2
- 2 Lower lobe of superior appendage with black, sub apical, sclerotised tooth and pointed tip.....sinclairi n.sp
 Lower lobe of superior appendage without sclerotised, sub apical tooth, unicolorous red.....3
- 3 Pointed tip of lower lobe drawn into a massive projection; thorax with characteristic black spot below metathoracic spiracle, (Chatham Islands only).....tuanuii
 Pointed tip of lower lobe not drawn into a massive projection; thorax lacking such a black spot.....zealandica

TENTATIVE KEY TO FEMALE HETEROCHROME MORPHS

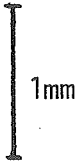
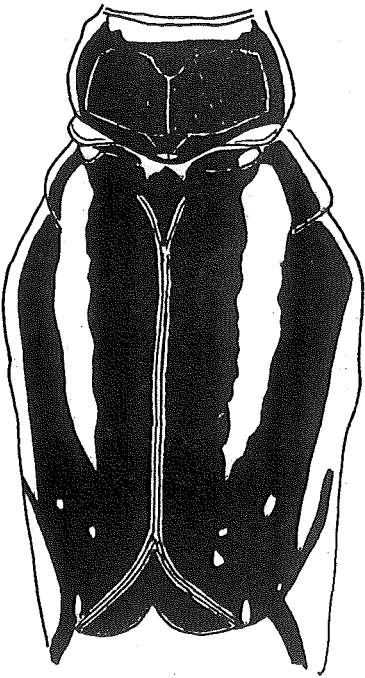
- 1 With black spot below metathoracic spiracle (Chatham Islands only)
tuanuii
 Without such a black spot, not from Chatham Islands.....2
- 2 Length of body about 38 mm, mesepisternal markings reddish, pale anterior 'rings' of abdominal segments 3-7 narrow, incomplete, with large dorsal break (Fig. 5).....sobrina
 Not as above, length of body less than 36 mm, mesepisternal markings yellowish, 'rings' of abdominal segments 3-7 broad, almost complete (Fig. 5).....zealandica, sinclairi

Fig. 5. Females of X. zealandica and X. sobrina:

- a) Female X. zealandica from Manganoho. Lateral view and dorsum of abdomen.
- b) Female X. sobrina from Waipoua F. Lateral view and dorsum of abdomen.
- c) X. zealandica: dorsum of head and thorax of an aberrant female from Kopuku. The colour pattern differs more from that of a typical X. zealandica than did the specimen described as antipodum.



c



FINAL INSTAR LARVAE

- 1 From the Chatham Islands; labial palps with 7 setae, prementum with 4 setae (per side).....tuanuii
From the main islands of New Zealand and off shore islets.....2
- 2 Labial palp with 8 (sometimes 7) setae, prementum with about 5-7 setae in a row and sometimes with an additional 1-2 setae anterior to the medial end of this row, in tarns along South Island main divide (Fig. 6d, e, f).....sinclairi
Labial palp with 7 or fewer setae, prementum without additional setae anterior to main row (Fig. 6a, b, c).....3
- 3 Labial palp with 6 (sometimes 5 or 7) setae; prementum with 4-5 setae (per side), widespread.....zealandica
Labial palp with 5? setae; prementum with 4? setae (per side), inhabits streams in Kauri Forest areas (rare).....sobrina
(a single specimen only of this species has been examined)



Fig. 6. Labium and labial palp of X. zealandica and X. sinclairi exuviae. Fig. 6a, b, c X. zealandica, Cass; Fig. 6d, e, f X. sinclairi, type locality. Figs 6b, c, f detail of distal margin of palp.

DESCRIPTIONS

Xanthocnemis zealandica (McLachlan 1873)

Type locality: New Zealand (series of specimens used, probably from a variety of sites).

Type: LECTOTYPE male (designated Kimmins 1969), British Museum (Natural History).

For the preparation of the descriptions below males with anal appendages consistent with drawings of the types prepared by S. Brooks were used. Females taken in copula with such males were used to prepare descriptions of the female. Specimens from a variety of habitat types throughout the known range of the species were examined.

Male:

Size: body length 31.30 mm; S.D. 0.94 mm; forewing length 18.39 mm; S.D. 0.60 mm ($R_s = 0.59$); $n = 80$. Site Roxburgh pond, 50 collected on 20 Jan 1983; 30 collected on 22 Jan 1984. Body length in both samples showed slight polymodality under 1:3:1 smoothing*, forewing length was unimodal. The sample of 20 Jan 1983 contained two 'short' individuals (body lengths 28.7, 29.2 mm but with wing lengths within one standard deviation of the mean). Larger individuals (to body length 35.1 mm) have been found. Animals from subalpine South Island sites are up to 20% broader than animals from lowland sites, but there does not appear to be any corresponding increase in length.

Colour pattern:

HEAD

Labium: yellowish-buff.

Labrum: orange; large, black triangle basally, small black lateral markings.

* see appendix for discussion of smoothing technique

Postclypeus: anterior face and crest orange, with (variable) small black lateral stripe on anterior face [L. Poerua 6/6, Roxburgh 1/7]; dorsal surface bronze-black.

Frons: anterior area orange to line drawn through base of antennae.

Posterior area bronze-black.

Vertex: bronze-black. Small yellow splash in front of median ocellus.

Postocular lobes: bronze-black with large red-orange postocular spots (often bilobed) joined across base of occiput to give a 'dumbbell' appearance.

Antennae: second segment enlarged, orange; otherwise black.

Eyes: red.

THORAX

Prothorax: pronotum - anterior and posterior lobes orange, (posterior lobe sometimes black on dorsum). Midlobe bronze-black with large orange lateral triangles, vertices opposing; pair of small osculating middorsal orange triangles. Propleuron yellowish.

Synthorax: mesepisternum- dorsally bronze-black, posterior region of mid dorsal carina (pre alar sinus) orange. Broad, longitudinal, yellowish band, notched laterally at about 3/4 of its length. Laterally bronze-black. Mesepimeron- dorsally bronze-black with yellow longitudinal splash below notch in mesepisternal band. Ventrally yellow-orange (adjoining mesepisternal band dorsally). Metepisternum- yellow-orange fading to buff. Metepimeron- buff with small black marking on posterior lobe. Wingbase ridge and interpleural suture with black marking.

Metapleural suture with broad black spot near wingbase.

Legs: yellow-orange. Coxae with black markings, femora and tibiae with long black spines (decreasing in size towards tarsi). Tarsal articles with apical black rings.

Head and thorax with long brown-black setae.

Wings: venation reddish; pterostigma reddish-brown (yellowish in immature

specimens), costal and distal margins subequal, longer than proximal and anal margins.

ABDOMEN

Dorsally red with black markings as follows:

Seg. 1 with an anterior, dorsal black, bilobed spot (sometimes a pair of spots). Segs 7 & 8 with a pair of dorsal longitudinal bars (sometimes continued as pair of spots on apical area of seg. 6, on seg. 9 and at the anterior margin of seg. 10). Apical rings on segs 1-8.

Anal appendages: Superior appendage bifid, upper lobe subtriangular red with black sclerotised tubercle on dorso interior edge; black sclerotised tip, lower lobe with tip drawn into sharp point. Inferior appendage forcipate, about 2 x length of superior appendage, with black tip.

Colour variation

The 'appearance of two lines paler than the ground-colour' on the lateral thorax as cited in McLachlan's description is common on South Island specimens. Yellow and orange markings darken and redden with age and (in old individuals) the venation may become heavily infumed ('smoked').

Sources of material used in preparation of the above description (sample size in bracket): streamlet South Kaipara Head (2); L. Pupuke (3); streamlet Kopuku - Te Kauwhata (3); L. Waikare (1); ponds west of Tongariro (2); L. Rotoaira (2); stream Manganoho (1); Rakaia R. (at Rakaia) (5); L. Poerua (6); pond Roxburgh (7).

Further material from: Kaeo, Wairua Falls, Bethell's swamp, Morrinsville, New Plymouth, Marton, Oxford, Harihari, L. Ianthe and L. Onslow was checked against the prepared description.

Female heterochrome:

Size: body length 31.76 mm; S.D. 1.22 mm; forewing length 20.02 mm; S.D. 0.85 mm ($R_s = 0.70$); $n = 20$. Site Roxburgh pond, 22 Jan 1984. Body length samples showed bimodality under 1:3:1 smoothing, forewing length was unimodal. Body length ranged from 28.6 – 34.1 mm. Larger individuals (to body length 35.8 mm) have been found. Animals from subalpine South Island sites are up to 20% broader than animals from lowland sites but there does not appear to be any corresponding increase in length.

Colour pattern:

General groundcolour of females yellowish-buff, in contrast to the orange-red of males. Head and thoracic colour patterns more variable than in male.

HEAD

Labium: as for male.

Labrum: black marking varies from similar to that of male [9/30] to a broad black basal band [12/30].

Postclypeus: similar to male.

Frons: similar to male.

Vertex: similar to male [2/30 lack yellow splash in front of median ocellus].

Postocular lobes: the extension of the yellow line across the occiput [missing in 1/30] variable, often thick and bifurcated [11/30] but may be reduced, thin and broken or even absent.

Antennae: as for male [16/30], or second segment dark red [10/30], or with orange band, or all orange [2/30].

Eyes: brown.

THORAX

Prothorax: pronotum— anterior and posterior lobes yellowish. Midlobe similar to male [15/30], with single middorsal spot [2/30], without middorsal markings [12/30], without markings [1/30].

Synthorax: mesostigmal plates with yellow tips, otherwise similar to male. Some animals [3/30 in this sample, but usually fewer] have the dorsolateral areas of the thorax black (see Fig. 5).

Legs: similar to male, femora with broad, dorsal, dark brown, blotchy markings forming a pair of broken lines.

ABDOMEN

Dorsally dark bronze-black, ventrally pale gray often with yellowish tint. Segments 3 - 7 with ventral colour projecting dorsally to form anterior rings. Rings on 4 - 7 complete except for very narrow, middorsal black line [ring on segment 3 complete in 1/30]. Segment 10 excised dorsally with an often broad, yellowish posterior border; colour occasionally with anterior extension to 9.

Anal appendages: pale [19/30], darker than ventral abdomen colour [10/30], nearly as dark as dorsal colouration [1/30]. Styles: dark brown. Colour variation

The extent of the yellow markings on females appears to vary. The most extreme reduction in yellow markings found in this survey (Fig. 5) appears more extreme than the specimen described as X. antipodum by Selys. Tillyard's (1913a) synonymisation of X. antipodum within X. zealandica is appropriate.

Sources of material used in preparation of the description (sample size in bracket): Kaiwi Lakes (2), Western Springs (1), Kopuku-Te Kauwhata (1), Karapiro (1), Manganoho (2), Rakaia (1), L. Poerua (5), R. Avon (3), Omakau (1), L. Onslow (3), Roxburgh (8), Bullock Ck (1), Mandeville (1)

Female androchrome:

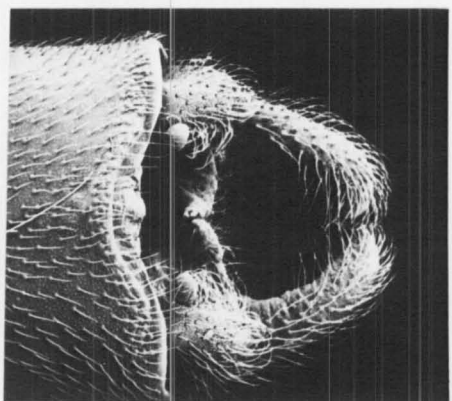
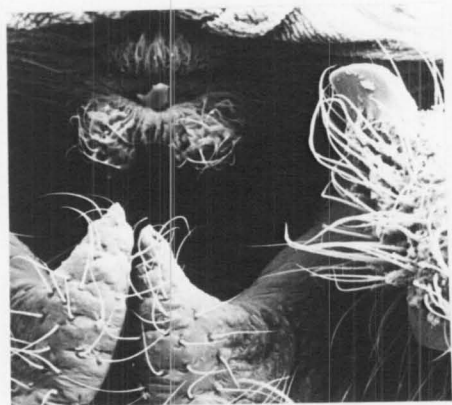
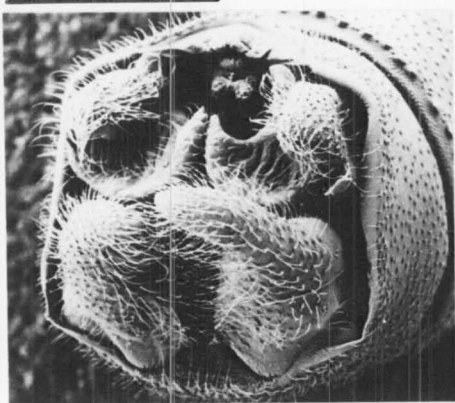
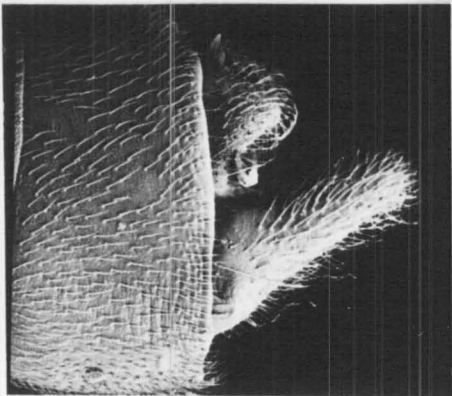
Size: body length 32.20 mm; S.D. 0.96 mm; forewing length 19.80 mm; S.D. 0.44 mm ($R_s = 0.75$); $n = 8$. Site Roxburgh pond, on 22 Jan 1984.

Female androchromes resemble males closely in head and thoracic colour patterns. The abdominal pattern involves larger, more conspicuous and

Fig. 7. Anal appendages of male X. zealandica? from Mandeville.

Top to bottom: lateral, caudal, caudal detail and dorsal views.

(scale bars = 0.5mm)



more intricate areas of black markings than in males. These patterns are highly variable even at one site.

Comments on morphometrics.

Significant differences in body length were found between the two collections of males and the heterochrome and androchrome females from the Roxburgh site ($F_{[3,104]} = 2.937$, $P \leq 0.036$). Analysis by orthogonal contrasts indicated sexual dimorphism was significant ($P \leq 0.02$). A highly significant difference occurred between male and female forewing lengths ($F_{[3,104]} = 15.05$, $P \leq 4 \times 10^{-6}$). There was no significant difference between either body or forewing length of the two female morphs ($F_{[1,26]} < 1$).

Status.

Even after the removal of X. sobrina, tuanui and sinclairi, zealandica still contains considerable 'variation'. In the Southland/Stewart Island region males with anal appendages as extreme as those in Fig. 7 were collected in the same localities as animals whose anal appendages were indistinguishable from those in Fig. 3. Within this 'species' there is still variation which may be taxonomically significant.

Biology.

X. zealandica is found through much of New Zealand occupying a wide variety of habitats. The species breeds in ponds, streams, swamps, along lake margins and in slack water at the sides of large rivers. If, as it appears, the species is associated with 'open country' there would have been marked increases in the habitat available after the Polynesian fires of the 10-11 th centuries and again after land clearing by European settlers (McGlone 1983).

X. sobrina (McLachlan 1873)

Type locality: New Zealand (probably Bay of Islands).

Type: HOLOTYPE male British Museum (Natural History).

Male:

Size: body length 39.00 mm; S.D. 0.95 mm; n = 11; forewing length 23.55 mm; S.D. 0.58 mm; n = 8.

The colour pattern closely resembles that of male X. zealandica. Points of difference are as follows:

Ground-colour generally a richer, darker red than X. zealandica.

HEAD

Labium: margins orange, central area grey.

Labrum: lateral black markings reduced.

Vertex: [17/18] without yellow splash in front of median ocellus; [1/18] splash very small (barely discernible at 25X).

THORAX

Metepisternum ground-colour red, metepimeron ground-colour pale grayish; colour transition at suture abrupt.

Wings: pterostigma often covering 1.25 - 1.5 cells. 16 - 18 postnodals.

ABDOMEN

Seg. 1 with an anterior pair of black spots [8/10]; single spot [2/10].

Anal appendages: Superiors fully half length of inferiors, trapezoidal in dorsal view, lower edge strongly concave, lower lobe without pointed tip, single sharp subapical tooth. Colour pattern and tubercles similar to X. zealandica. Inferiors similar to X. zealandica, apices converge sharply.

Sources of material used (sample size in bracket): Waipoua Kauri Forest (16); Trounson Kauri Forest (2)

Female heterochrome:

Size: body length 37.66 mm; S.D. 0.80 mm; forewing length 24.40 mm; S.D. 0.21 mm; n = 5.

The colour pattern resembles that of female X. zealandica. Points of difference as follows:

Ground-colour generally richer and redder than X. zealandica.

HEAD

Labrum: [4/6] with at least basal half black, [2/6] similar to X. zealandica.

Vertex: yellow splash in front of median ocellus reduced [3/6] or absent.

Post ocular lobes: yellow marking reduced to narrow line.

THORAX

Synthorax: mesostigmal plates blackish [4/6], with yellow marking [2/6]. no yellow on dorsal carina.

Legs: dorsal half of femora black.

ABDOMEN

Anterior extensions of lateral colouring reduced, not meeting dorsally (Fig. 5). Segment 10 without yellowish posterior border [5/6].

Anal appendages: dark.

Source of material examined: Waipoua Kauri Forest (6 specimens).

Female androchrome:

Unknown.

Notes: The type bears a label 'militare' in Adam White's script (S. Brooks pers. comm.) and it can be assumed with some confidence that X. sobrina was included in Andrew Sinclair's collection referred to by White (1843).

Credit for the rediscovery of X. sobrina belongs to J.S.

Armstrong who found individuals in the Waipoua Forest and others near the Kaueranga R., Coromandel Penn. I have since found the species at the

Trounson Kauri Forest Park, at the Kaiwi Lakes, and at Okahukura near Taumaranui.

Status.

This species has been collected in a few North Island forest habitats, and should be sought in other remnant forests. The known Kauri forest habitats are protected as much as is practicable, by having reserve status. However, it is unclear whether X. sobrina still occurs at the Kaiwi lakes. During the early 1970s, rainbow trout (Salmo gairdneri) and later 'mosquito fish' (Gambusia affinis) were liberated in the habitat and the numbers of all dragonfly species decreased markedly. Habitat modification through runoff of agricultural fertilisers and conifer forestry about the lake shore also has occurred over the past 15 years. Formerly the lakes were cool and oligotrophic with negligible aquatic vegetation. Over the last decade there have been widespread encroachments of marginal vegetation. These have limited water circulation in the shallows and increased algal cover near the shoreline with a consequent increase in solar energy absorbed.

Xanthocnemis collected from other sites in Northland (e.g. Spirits Bay, Kaeo, Whangarei, Wairua Falls) have proved to be X. zealandica. X. zealandica occurs also at the Kaiwi Lakes and on the Waipoua R. in the middle of the Kauri forest.

Until the widespread clearing of forest in the later nineteenth century X. sobrina was probably widespread through northern New Zealand. Its presumptive occurrence in Andrew Sinclair's collection, and the further specimens forwarded to the British Museum prior to 1894 attest to this. The apparently limited geographical distribution of the species, rapid reduction of habitat (hence abundance) and lack of collecting in the north help explain the failure of later workers to obtain specimens of X. sobrina and its subsequent 'loss' from the literature.

Biology.

In the laboratory, 2nd instar X. sobrina developed at 16°C, but died when held above 20°C (cf X. zealandica which develops successfully at 25°C). Should this limit apply in the field, then the restriction of the species to cool, heavily shaded forest streams and a cool lake system is understandable. Later instars appear more temperature tolerant.

In many insects the occurrence of larger adults is associated with cooler larval habitats and it might be supposed that the size of X. sobrina adults may be a consequence of development patterns in the cool water systems they inhabit. A few X. sobrina larvae raised to the 8th instar were consistently larger (instar for instar) than X. zealandica raised under the same conditions. X. zealandica from cool springs, mountain tarns and bogs with temperature regimes similar to, or even colder than, X. sobrina larval habitats do not grow as large as X. sobrina.

X. tuanuii Rowe 1981

Type locality: brown water stream, Chatham Island near 44°04'S, 176°38'W.

Type: HOLOTYPE male Auckland Institute and Museum. Allotype taken in cop with holotype, Auckland Institute and Museum.

A detailed description of this taxon has been published recently (Rowe 1981) (bound in on page 37).

In both sexes the colour pattern closely resembles that of X. zealandica. The main point of difference is the presence of a diffuse black spot below the metathoracic spiracle.

Male anal appendages: superiors fully half length of inferiors, lower edge strongly concave, lower lobe with massively pointed tip. Colour pattern and tubercles similar to X. zealandica. Inferiors similar to X. zealandica, apices converge sharply.

X. sinclairi n.sp.

Type locality: tarn in the valley of the Louper stream below Whitcombe

Pass (43°13'S 170°58'E) ca 1250m ASL.

Type: HOLOTYPE male Auckland Institute and Museum. Allotype taken in
cop with holotype, Auckland Institute and Museum.

Male:

Size: body length 32.4 mm; S.D. 0.85 mm; n = 6

The colour pattern closely resembles that of male X. zealandica. Points of difference are as follows:

Overall more 'hirsute' than X. zealandica.

HEAD

Labium: pale yellow, covered in long pale setae.

Antennae: anterior face basal and second segment red.

Area behind eye all pale yellowish, strongly setose (cf. X. zealandica with narrow yellow rim about eye, otherwise dull brown-black to neck, not markedly setose).

THORAX

Legs: covered in fine white setae length about that of spines.

Wings: pterostigma often covering 0.8 cell.

ABDOMEN

Anal appendages: superiors short, rounded in dorsal view, upper lobe similar to X. zealandica, lower lobe with subapical 'tooth' and pointed tip. Colour pattern and tubercles similar to X. zealandica. Inferiors similar to X. zealandica, apices converge sharply.

Female:

Size: body length 32.7 mm; S.D. 1.0 mm; n = 4

The colour pattern closely resembles that of female X. zealandica.

Points of difference as for male.

Material examined: 7 males, 7 females, from tarns near type locality.

Notes: this species is named in honour of Dr Andrew Sinclair (1794–1861), a pioneer, amateur scientist who was the original collector of most of the New Zealand endemic dragonfly species. Dr Sinclair drowned on 18 March 1861 while exploring the headwaters of the Rangitata R. in the company of Julius von Haast. The spot where Sinclair met his death is about 15 km from, and about the same altitude as, the type locality of this new species.

The holotype and allotype were collected by Margot and Peter Syme during an Auckland University Tramping Club trip over the Whitcombe Pass, and the tarns below the pass are the only known habitat of the species. Status.

Animals with the colour pattern characteristic of this taxon but without the subapical 'tooth' on the lower lobe of the superior appendage were found near the type locality. The tip of the lower lobe on these animals did not have the shape associated with X. zealandica. There may be some degree of hybridisation occurring but this could not be determined. The extremely harsh conditions of the larval habitat (probably fewer than 50 frost free days per annum, subject to snow at any time of year) would indicate that special adaptations were required and exuviae collected were morphologically different from those of X. zealandica. Xanthocnemis were sought throughout the trip on which X. sinclairi were collected. The nearest collections to the X. sinclairi site were made 5 km away, at 750 m ASL, on seepage areas above the Rakaia R; these specimens were typical of X. zealandica. Although recorded only near the type locality, X. sinclairi may well be more widespread, as little collecting has been done at this altitude. It would not be surprising if the distribution eventually proves to be similar to that of the mountain butterfly Erebiola butleri Fereday, which occurs in snow tussock country along the central and southern areas of the main divide of the Southern Alps (Gibbs 1980). While the distribution is obviously

restricted, the harsh climate and remoteness of the habitat have served to protect this species from interference.

Larval habitats were shallow (≤ 50 cm deep), flat rock bottomed depressions, probably seepage fed, with no aquatic macrophytes. Oviposition into fallen, waterlogged stems of tussocks at the edge of the tarns was observed and emergence had occurred on vertical cracks and shattered ledges of rough boulders and rock faces which formed the margins of the tarns. Four of seven exuviae recovered from rock faces were facing vertically head down. Larval behaviour observed in the field was very different from that of the other Xanthocnemis species. Thus, many X. sinclairi larvae were swimming spontaneously and freely through the open water of the shallow tarn, whereas larvae of the other species are cryptic, thigmotactic and inactive (see Chapter 8).

Table 1. The numbers of heterochrome and androchrome females in different Xanthocnemis species.

The X. zealandica material was obtained from a random sample; for the other species the total collections of females were used. F(x) is the calculated frequency of the androchrome gene in the population assuming it is a Mendelian recessive condition as found by Johnson (1975) in Ischnura damula and I. demorsa.

Species	No. heterochrome	No. androchrome	F(x)
<u>X. zealandica</u>	157	29	0.395
<u>X. sobrina</u>	12	0	0
<u>X. tuanuii</u>	7	8	0.73
<u>X. sinclairi</u>	9	15	0.79

Chi square test of association $X^2 = 39.43$, 3 dof; $P < 0.0001$

Table 2. Measure of similarity* in androchrome morph frequency between species.

Species	<u>X. zealandica</u>	<u>X. sobrina</u>	<u>X. tuanuii</u>	<u>X. sinclairi</u>
<u>X. zealandica</u>	1	0.25	0.0005	0.0001
<u>X. sobrina</u>		1	0.005	0.0005
<u>X. tuanuii</u>			1	0.5
<u>X. sinclairi</u>				1

* probability of homogeneity using 2 x 2 Chi square pairwise.

The total numbers of X. sobrina shown in Table 1 include the 6 females used in preparing the description plus 2 females observed but not captured 9 Jan. 1967 and 4 females observed but not captured 18 Feb. 1983 (all at the Waipoua Forest site). This is a conservative figure because it makes no allowance for the observations (and captures?) made by J.S. Armstrong which formed the basis for his assertion (Armstrong 1975/80, p6) that the androchrome morph did not occur, or else was very rare, in this species.

The frequency of occurrence of the androchrome morph varied significantly between the different species (Table 1). On the basis of the available data on androchrome morph frequencies X. tuanuii and X. sinclairi cluster out, then X. zealandica and X. sobrina (Table 2.). If Armstrong's assertion proves to be true, then X. zealandica, X. tuanuii and X. sinclairi will cluster out, leaving X. sobrina. The inhomogeneity of the colour morph frequencies, with the androchrome interpreted as a genetic marker, indicates a high probability that these taxa are isolated reproductively. The two most similar species X. tuanuii and X. sinclairi are isolated spatially.

DISCUSSION

The extremely limited odonate fauna of New Zealand has long been regarded as a biogeographical puzzle (McLachlan 1873, 1894, Miller 1955, Lieftinck 1975, Watson 1981). The antiquity of the Odonata (Carpenter 1977, Wootton 1981) and the geological history of the New Zealand landmass (Stevens 1980) indicates that New Zealand's original faunal inheritance must have been very much more extensive, and richer, than the extant fauna indicates. The peculiarities of the present New Zealand fauna are probably a consequence of historical conditions during the Pleistocene ice advances. Palaeoclimatic evidence (Stevens 1980) indicates that a long warm temperature period occurred from the time New Zealand separated from Gondwana until the Pleistocene. In contrast to continental areas, the biota of New Zealand would have had only restricted opportunities to 'retreat' along latitudinal gradients during glacial advances to new temperate zones, nearer the equator. Poikilotherms, especially those dependent on still water habitats, must have been particularly vulnerable to widespread extinction during glacial advances. There are coenagrionid faunas extant which flourish under climatic conditions more extreme than occurred in New Zealand during the Pleistocene (e.g. in Canada); however, the New Zealand pre Pleistocene fauna would have been adapted to warm-temperate conditions (Stevens 1980). Current opinion is that the onset of Pleistocene glaciations was rapid. Warm-temperate species were unlikely to have been preadapted to survive such an environmental change. The lack of radiation among the Odonata present in New Zealand is also hard to explain. The geological time scales of the Hawaiian Islands, Fiji and Samoa indicate that even in relatively small areas (about 16 000, 18 000 and 3 000 km², respectively) coenagrionids can radiate considerably within a period of less than 7 million years. The Hawaiian Islands with an area of about 16 000 km² and an age \leq 7MY have 34 species in the endemic pseudagrionine genus

Megalagrion (Davies 1981); Fiji (area about 18 000 km²) has > 50 species of Nesobasis (Davies 1981, Donnelly 1983); Samoa (area 3 000 km², age < 7MY) has 10 endemic species, including 2 species in each of 2 endemic genera (Fraser 1927, 1953). However, these Pacific islands were not subjected to intense climatic stresses during glacial advances. The occurrence of speciation within Xanthocnemis indicates that the New Zealand fauna is not as peculiar as was previously considered.

The radiation that has occurred within Xanthocnemis is recent and probably originated in the (late) Pleistocene. X. sobrina appears to be a cold stenothermic species largely restricted to shaded forest streams in the northern (warmest) part of the country. X. tuanuii occurs on Chatham Island (and probably nearby islets) which were not glaciated during recent advances (Stevens 1980). X. sinclairi is a cold adapted high subalpine species. The ubiquitous X. zealandica originally may have been associated with open country habitats such as swamps and grasslands. The massive increase in area of these habitats following large scale burnoffs during Polynesian settlement (about 1000 YBP) and land clearing for pastoral purposes in historical times would have provided the opportunity for a species dependent on open country to expand its range and numbers markedly.

There remain forms of uncertain taxonomic status. In Southland, Stewart Island and at least some off lying islets (e.g. Codfish I.), males occur with different superior appendages (Fig. 7). In places (e.g. Mandeville, Codfish I.), and perhaps throughout their range, they are sympatric with typical X. zealandica. While under the stereomicroscope these appendages resemble those of X. tuanuii superficially in that the tip is drawn into a massive projection, detail revealed by the SEM indicates a close similarity to those of X. zealandica (e.g. shape of the projection, presence of setae). Whether these forms represent an extreme morph of X. zealandica or a distinct species is undetermined.

A NEW SPECIES OF *Xanthocnemis* Tillyard (ODONATA: COENAGRIONIDAE) FROM THE CHATHAM ISLANDS, NEW ZEALAND

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Abstract. *Xanthocnemis tuanuii* n.sp. is described from Chatham Island, New Zealand. It is closely related to the New Zealand mainland species *X. zealandica* but differs largely in the form of the male superior appendages. There also appear to be consistent differences in colour pattern.

The earliest description of a New Zealand Coenagrionid was that of *Telebasis zealandica* by McLachlan (1873). Tillyard (1913) subsequently erected the genus *Xanthocnemis* for McLachlan's species and synonymized other species which had been described from the main islands of New Zealand (*Telebasis sobrina* McLachlan, 1873, *Xanthagrion antipodum* Selys, 1876) with *X. zealandica* (these synonymies will be further discussed in a revision of the genus being prepared by the present author).

However, the Chatham Island *Xanthocnemis* was recognized as being different from those familiar to collectors on the main islands of New Zealand. Hutton (1898) noted differences and assigned Chatham Island specimens to *X. sobrina* (followed and quoted in Hudson 1904), and Tillyard (1913) commented on their large size, "specimens . . . from Chatham Island are exceptionally fine, and the largest of the whole series".

The Chatham Islands are 800 km east of the South Island, New Zealand. In January, 1980, I collected Odonata in the undisturbed rainforest area at the southern end of Chatham Island, which is the northern and largest island of the group. Differences between the *Xanthocnemis* population of that island and those of the main islands of New Zealand were noted during field observations; and from further morphological examination it is concluded that this island population warrants specific recognition. *X. zealandica* was not found on Chatham Island.

***Xanthocnemis tuanuii* Rowe, sp.n.**

(Figs. 1-6)

MALE (based on 11 specimens)

Length 33 - 36 mm (anterior margin of head — posterior margin of abd X).

Head. Labrum buff with three triangular basal black spots, lateral spots sometimes reduced. Postclypeus yellow-orange. Frons bronze-black. Vertex, anterior area orange; base bronze-black, the straight or slightly convex division lying below antennae. Epicranium bronze-black with pair of large red postocular spots joined by red line across posterior margin to form a "dumb bell". Postocular spots sometimes bifurcated or reduced. Antennae with orange distal annulus on basal segment; second segment large, usually red; other segments bronze-black. Eyes red. Back of head pale with small elongated yellow-orange splash on eye margin. Frontal and dorsal surfaces with thick covering of long black hairs.

Prothorax. Anterior lobe orange. Dorsum bronze-black with lateral orange triangles, vertices opposing. Two osculating orange spots on posterior area of central lobe (missing in one specimen). Lateral areas orange. Posterior lobe narrow, orange with fringe of long black hairs; central area of posterior lobe black in one specimen.

Synthorax. (Fig. 1). Mesepisternum, mesepimeron bronze-black with orange markings; ventrally yellowish-buff. Diffuse black spot below metathoracic spiracle. Prothorax and synthorax closely covered with long black hairs overall.

Legs. Coxae and trochanters orange with black markings. Femur and tibia red-orange with small black basal markings and two rows of long black spines.

Wings. Hindwing length 18.5 - 20.5 mm. Venation dark red-brown. Pterostigma red, covering $1\frac{1}{2}$ (rarely 1) cells.

Abdomen. Red with black (dorsal) markings as follows. Abd I with bilobed basal spot (absent in 2 of 11 specimens). Abd II-V with apical rings. Abd VI with apical spots and incomplete ring (markings fused in 3 of 11 specimens). Abd VII with pair of longitudinal bars and apical ring, 9 of 11 specimens with a narrow red expansion to produce a red \dagger dorsal mark. Abd VIII with pair of longitudinal bars. Abd IX, X with basal spots (absent in 2 of 11 specimens). Abd I, II covered in long black hairs.

Anal appendages. (Figs. 2-5). Superiors bifurcated. Upper lobe red-orange with heavy black dorso-interior spine and small black ventrodistal spine. Lower lobe paler. Massive, especially in caudal view, converging, tips opposing, tip drawn into massive dorsally directed projection. Inferiors approximately $1\frac{1}{2}$ x length of superiors, red-orange, forcipate, opposing tips black.

Penis. Broader than in *X. zealandica*, shaft with lateral flanges lying below curved horns of glans (Fig. 6).

FEMALE heterochrome (based on 4 specimens)

Head. Labrum buff with broad black basal line. Postclypeus buff. Frons bronze-black. Epicranium as for male except "dumb-bell" buff. Antennae as for male.

Prothorax. Dorsally bronze-black with yellow lateral surfaces. Anterior lobe broad, yellow. Central lobe with yellow lateral spots. Pair of central spots on posterior edge of central lobe in 2 of 4 specimens. Posterior lobe narrow, yellow with fringe of long black hair.

Synthorax. Largely as for male but markings yellow on bronze-black. Large yellow triangle with apex directed posteriorly at centre of anterior edge of mesepisternum.

Legs. Yellow with heavy black markings. Femur with broad, black, exterior line. Spinose.

Wings. As for male.

Abdomen. Dorsally bronze-black, ventrally and laterally yellow. Abd I with (in 3 of 4 specimens) a yellow spot at posterior dorsal margin. Abd III - VI with incomplete yellow rings at anterior edge.

FEMALE androchrome (based on 6 specimens)

Colour pattern largely as in male with the following exceptions.

Head. Labrum buff, basal spots joined by basal black line. Epicranium postocular spots reduced.

Prothorax. Central spots on posterior margin of median lobe frequently absent.

Synthorax. Large red triangle at anterior edge of mesepisternum.

Abdomen. Black markings on abdomen considerably more extensive than in male. Abd VIII - X dorsally black.

Specimens examined. Holotype ♂, Allotype ♀ androchrome, taken in copula. CHATHAM I: brown water, forest stream on southern bank of Tuku a tamatea R, approximately 800 m into the forest east of the ornithologists' camp 'Tuku Base', near NZMS 240 879916 (interpolated), approximately 44°04'S, 176°38'W, 22.I.1980, R.J. Rowe. Both deposited in Auckland Institute and Museum.

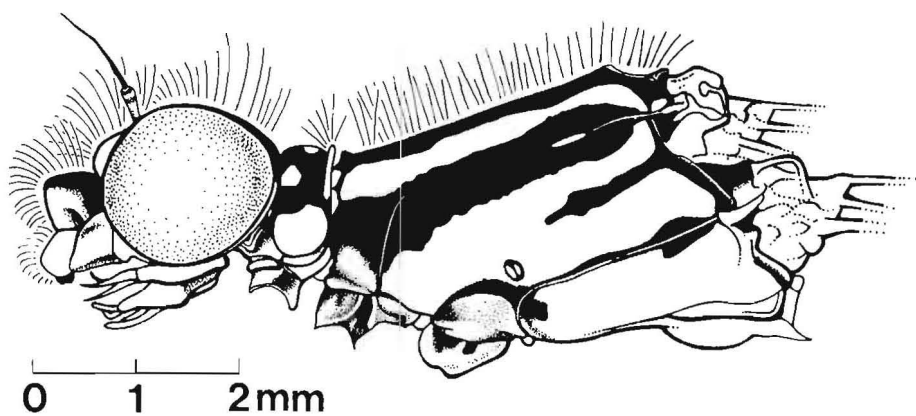
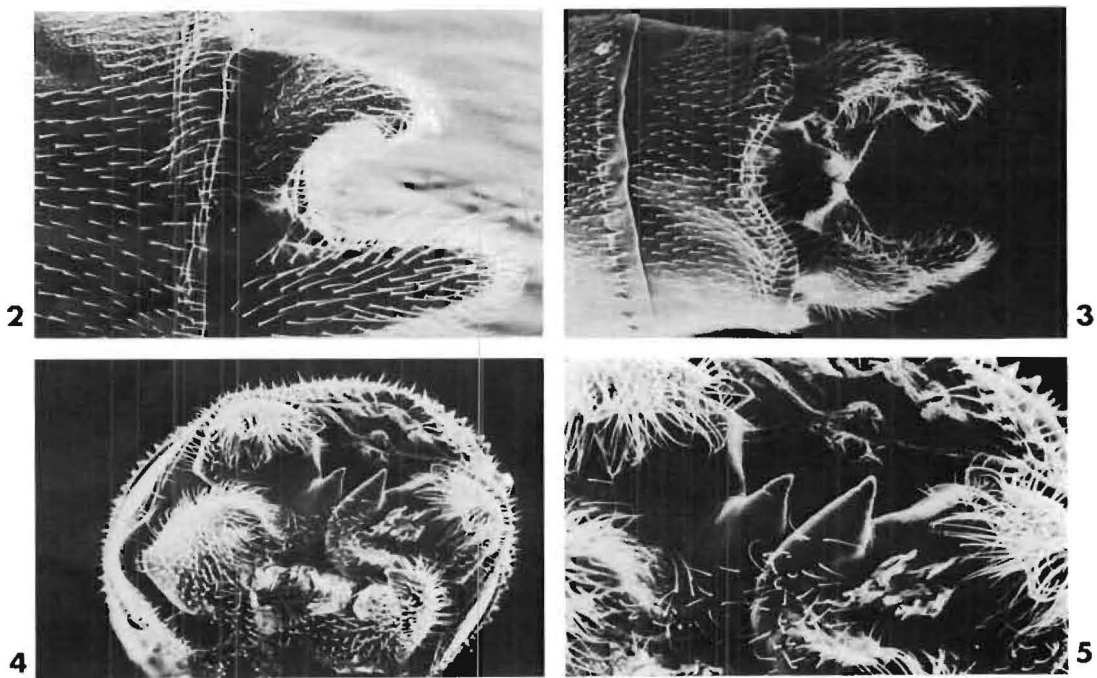


Fig. 1. *Xanthocnemis tuanuii* n.sp. Holotype ♂. Head and thorax, lateral (length of dorsal hairs indicated).



Figs. 2-5. *Xanthocnemis tuanuii* n.sp. ♂ from 'Tuku Base'. Anal appendages. 2. Lateral. 3. Dorsal. 4. Caudal. 5 Caudal, detail.

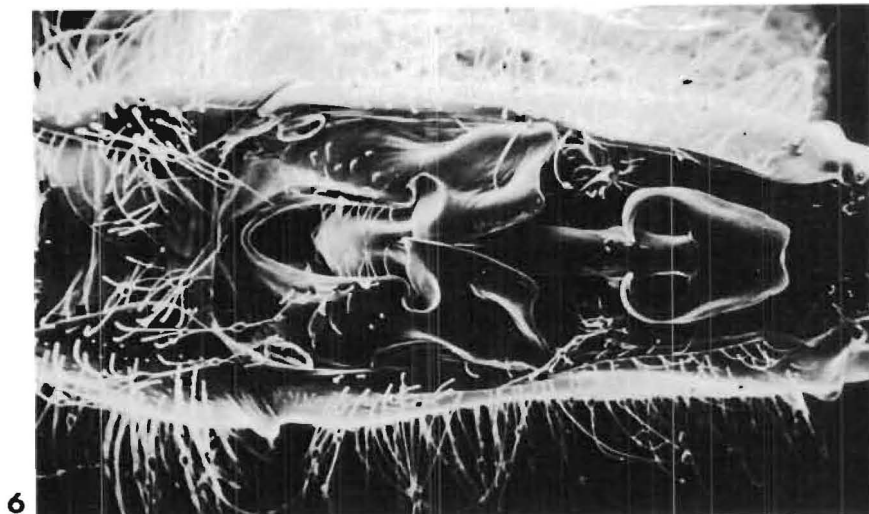


Fig. 6. *Xanthocnemis tuanuii* n.sp. ♂ genitalia, ventral.

Paratypes. Five pairs taken *in copula*, same data as holotype. Deposited in: Auckland Institute and Museum; Entomology Division D.S.I.R.; Canterbury Museum; British Museum (Natural History); Australian National Insect Collection, C.S.I.R.O. Four males, same data as holotype, retained in the author's collection.

Other material. CHATHAM I. (Canterbury Museum) 3 ♂♂, 1 ♀, Chatham, 24 I. 1924, C. Lindsay. (D.S.I.R. Entomology Division) 3 ♂♂, 2 ♀♀, L. Te Roto, Awatotara Tableland; 2 ♂♂, 1 ♀, Kaingaroa, Waitangi, -II. 1967, G. Ramsay; ♂, ♀ Awatotara, Waikato Pt., -II. 1967, G. Kuschel. (Rowe Collection) 6 ♂♂, 5 ♀♀, Tuku a tamatea R., bush runnels near Tuku Base, -I. 1980, R.J.R.

Neither Hutton's (1898) material nor the material viewed by Tillyard could be located.

The most obvious point of contrast with *X. zealandica* (McLachlan) is the shape of the male superior appendage; this difference is especially apparent in the caudal view of the lower lobe. Lateral flanges on the penis are absent in *X. zealandica*. In colour pattern, the diffuse black spot below the metathoracic spiracle appears to be absent in all *X. zealandica* examined, and *X. tuanuii* is markedly more hairy than *X. zealandica*. In the female the pair of large triangles at the dorso-anterior edge of the synthorax of *X. tuanuii* is a distinguishing character. The high frequency of the female androchrome morph in *X. tuanuii* (8 of 14 in the sample collected) contrasts with *X. zealandica* where this morph makes up approximately 20% of the population.

The name *tuanuii* is proposed for this species in honour of Mr Manuel Tuanui of Chatham Island.

Acknowledgements. Mr Manuel Tuanui and his family have been extremely helpful to biologists working on Chatham Island from 'Tuku Base', which is situated on Mr Tuanui's farm. Mr David Crockett (leader) and members of the 1980 construction party of the Ornithological Society Taiko Expedition (R. Cotter, R. Crockett, A.H. & A. Gordon, D. & L. Lowrie, T. O'Brian and R. Thomas) were also all immensely helpful on Chatham Island. I thank the Canterbury Branch of the Royal Society of New Zealand for a travel grant which made my trip possible; the University of Canterbury assisted with the provision of transport. The late John S. Armstrong, of Taupo, provided the original impetus to this study; Mr D.E. Kimmins and Mr S. Brooks, British Museum (Natural History), London, England, patiently answered queries and provided drawings of type appendages. Dr M.J. Winterbourn, Mr P.M. Johns, University of Canterbury, Christchurch, and Dr J.A.L. Watson, Division of Entomology, C.S.I.R.O., Canberra, Australia, kindly commented on a draft manuscript. Peter Quin, per Auckland Museum, kindly illustrated the head and thorax.

REFERENCES

- HUDSON, G.V.
 1904 *New Zealand Neuroptera*. West, Newman, London. 102p., 11 pl.
- HUTTON, F.W.
 1898 On a collection of insects from the Chatham Islands with descriptions of three new species. *Trans. Proc. N.Z. Inst.* 30: 155-160.
- McLACHLAN, R.
 1873 A catalogue of the neuropterous insects of New Zealand, with notes and descriptions of new forms. *Ann. Mag. Nat. Hist.* (4)12: 30-42.
- TILLYARD, R.J.
 1913 On some new and rare Australian Agrionidae. *Proc. Linn. Soc. N.S.W.* 37: 403-479.

Section 2: Displays

The unexpected discovery of agonistic displays in Xanthocnemis zealandica larvae (Rowe 1978a), was the first unequivocal demonstration of territorial behaviour in Odonata larvae. Prior to this discovery, Machado (1977) had found that large larvae of Roppaneura beckeri Santos (Zygoptera: Protoneuridae) displaced others from the leaf-axil water pockets used as habitat and Macan (1977) had postulated that some form of territorial exclusion might be responsible for larvae of Pyrrhosoma nymphula (Sulzer) (Zygoptera: Coenagrionidae) exhibiting both two and three year life cycles in the same habitat. Prodon (1976) sought, but did not find, territorial behaviour in Cordulegaster boltoni (Donovan) (Anisoptera: Cordulegasteridae). A reinterpretation of Tillyard's (1916) observations of Aeshna brevistyla Rambur (Anisoptera: Aeshnidae) larvae in aquaria suggest that territorial behaviour might occur in that species as well.

A large display repertoire and the use of considerable time displaying indicate that strong adaptive pressure presumably existed for the evolution of these behaviours. In Chapter 2 the display repertoire and the ontogeny of agonistic displays in X. zealandica is documented to provide a basis for evaluating the importance of these activities in the larval life-history and, by association, to indicate their possible adaptive features.

Many coenagrionid larvae are known to spend much of their time swinging their abdomens laterally (Corbet 1962). Previously this had been regarded as a purely respiratory activity. The (unsuccessful) attempts to induce the behaviour by placing X. zealandica larvae under severe respiratory stress are documented in Chapter 3.

CHAPTER 2

Intraspecific interactions of New Zealand damselfly larvae –
Xanthocnemis zealandica, Ischnura aurora and Austrolestes colenisonis

INTRODUCTION

The depauperate Odonata fauna of New Zealand (Lieftinck 1975) includes six species in the suborder Zygoptera. The endemic genus Xanthocnemis (Coenagrionidae: Pseudagrioninae) contains four species (Chapter 1). X. zealandica (McLachlan) is widely distributed and very common in both lentic and lotic habitats while three sibling species (X. sobrina (McLachlan), X. tuanuii Rowe and X. sinclairi Rowe) are confined to restricted small regions of generally unmodified habitat (Rowe in press). Ischnura aurora aurora (Brauer) (Coenagrionidae: Ischnurinae), a species with adaptations for transoceanic dispersal (Rowe 1978b), has become established in shallow, eutrophic habitats throughout the North Island during the last 60 years (Armstrong 1958b, 1975/1980; Rowe in press). Austrolestes colenisonis (White) (Lestidae: Sympecmatinae), an endemic species, is widely distributed and very common, especially in lentic habitats. The ecologies of the species are reviewed in Rowe (in press). The territorial behaviour of X. zealandica larvae has been described in a brief, preliminary note (Rowe 1980).

In the morphologically-based classification of the Odonata of Fraser (1957), the Coenagrionidae and the Lestidae are placed in widely separated branches of the Zygoptera. However, the subfamilial classification of Coenagrionidae erected by Fraser was primarily for taxonomic convenience and was not intended to indicate probable phylogeny. While the New Zealand fauna is limited, examples from two of

the four superfamilies of the Zygoptera were available for study.

In this chapter the displays and other behaviours exhibited during intraspecific agonistic interactions are described. The size of the display repertoire is closely comparable to that of a Holoplatys sp. (Araneae: Salticidae) (Jackson & Harding 1982), social insects and vertebrates (Wilson 1975), despite the fact that displays associated with courtship and mating are not present in the larval insect. The ecological correlates of these behaviours, and their potential adaptive significance, are discussed in section 5.

In the past there has been considerable debate over the function of the caudal lamellae of Zygoptera (Tillyard 1917, MacNeill 1960, Corbet 1962). Use in defence (Williams 1936, Corbet 1952) and swimming has been observed, but, in view of the extensive tracheation in many families, the consensus in the literature favours a primarily respiratory function (Corbet 1962). More particularly, the regular, lateral movements of the abdomen, observed in many members of the Coenagrionoidea (e.g. Platycnemidae Copera (Lieftinck 1940), Platycnemis (Corbet 1962); Coenagrionidae (Coenagrioninae) Pyrrhosoma (Lawton 1971a), Coenagrion (Baker 1981a), (Pseudagrioninae) Ceriagrion (Gardner 1956), Xanthocnemis (Rowe 1980), (Ischnurinae) Ischnura (this study)) have been interpreted as ventilatory movements (Lawton 1971a, Thompson 1978a, Baker 1981a). There is little experimental evidence for this. In the case of Xanthocnemis the stereotypy of the regular lateral movements, the 'unusual' postures adopted when exhibiting the behaviour, the responses of conspecifics and the fact that the behaviour is not shown in response to conditions of low oxygen tension indicate that these abdominal movements are intraspecific displays and not ventilatory movements.

In many investigations of insect, and other small arthropod, agonistic behaviours the experimental protocol has involved introducing one animal (the occupant) to an observation area and then, after a

variable (but generally short) interval, introducing a second animal (the invader) (e.g. Jansson & Vuoristo 1979, Baker 1981a, Jackson & Pollard 1982). The first interaction between the animals is then observed. The rationale behind this protocol appears to be the assumption that the animals will respond as simple automatons to the stimuli presented. The justification for this assumption seems to depend on an extension of Julian Huxley's 'one captain on the bridge at a time' simile (quoted in Lorenz 1967); animals are expected to behave as automatons, conducting one activity at a time, and that at a characteristic intensity regardless of 'extraneous' external conditions. As Lorenz comments the 'simile is very apt in some cases of animal behaviour in conflict situations' (my emphasis). The protocol, when applied to a fish, has been criticised (Dow et al 1976, Maynard Smith 1982) because it generates what are probably spurious results.

It was apparent that this protocol was not appropriate for studying X. zealandica. Animals moved gently either with forceps or in glass tubes settled very quickly on being placed in an observation chamber; however, after a short while they began to walk or swim about. Behaviours were often altered visibly, in seemingly unpredictable ways, for periods of many hours (or sometimes days) after the animal had been moved. Even animals made to move laterally about a perch sometimes abandoned their perch and wandered about. The initial period of quiescence after handling should probably be interpreted as a 'shock' effect; the reliability of observations made during this period is highly suspect. Because of these limitations a less intrusive method of initiating conflicts was used.

METHODOLOGY

Intraspecific interactions

Observations were made on X. zealandica larvae collected by dipnet from L. Pupuke, ponds and lakes near Cass, from ponds alongside the Waimakariri R. (43°24'S 172°40'E) and from ponds near Roxburgh

(45°29'S 169°19'E). Larvae both in and out of diapause (Deacon 1979) were used and no apparent differences were observed. Metabolic activity and behaviour of larval Coenagrionidae are similar in and out of diapause (Lawton 1971b, Deacon 1979); metamorphosis is blocked.

Approximate instar numbers were assigned to field caught larvae by comparing them with larvae raised from the egg. This degree of accuracy was considered appropriate as in many zygopterans the number of larval instars varies even between individuals from the same egg batch (Rivard & Pilon 1977, Pilon & Masseau 1983).

Standard 25 x 40 x 15 cm deep plastic aquaria were set up, each with 8 individually marked larvae (Rowe 1979) and 8 vertical plastic tube 'stems'. Other observations were made in small 15 x 4 x 15 cm deep glass cells with two larvae and one plastic stem. Small larvae were observed, approximately 20 at a time with 10 stems, in the glass cells. The aquaria were observed intermittently for over 600h and the glass cells for over 100h. Small larvae were observed for about 20h.

I. aurora larvae were collected at L. Pupuke and Bethel's swamp (36°54'S 174°27'E) and from ponds near Taupo (38°45'S 176°05'E). Observations (totalling about 20h) were made in the glass cells with two larvae and 4-6 stems.

A. colenisonis larvae were collected from L. Sarah and a pond near Cass and from ponds near the Waimakariri R. at Belfast. Observations were made under the same conditions as for X. zealandica. About 40h of observations were made.

It was discovered that stem diameter influenced the duration and character of contests and that consistent site defence usually occurred only after 24-48h occupancy (Chapter 8). Stems of 4.5 mm outside diameter were used for later instar X. zealandica and A. colenisonis. Stems of 2.2 mm outside diameter were used for young instar X. zealandica, I. aurora and when preparing some videotapes.

Larvae were allowed to initiate agonistic behaviours. Behaviours were sketched as they were observed and, in some cases, series of still photographs were taken. About 30h of videotape records were analysed to quantify some transitory behaviours (with a time resolution of about 0.04s (0.02s for large displacements)). Night-time behaviour was observed by silhouetting the larvae against a sheet of white paper which was weakly illuminated with a dim red light.

While conditions which allowed larvae to initiate encounters more closely approached conditions in the field than the common protocol, it was inefficient in its use of observer time and it also resulted in few contests being recorded in full. Events during initiation and termination of most contests were not observed because of the long duration of most interactions. Contests which involved few bouts were missed also (however, a number of these were observed in the small cells). Loss of time sequence information through inadequate knowledge of the history of the interaction was traded off against the 'natural' initiation.

RESULTS

In late instar X. zealandica, most observed contests consisted of a series of bouts usually lasting between 30s and 1h. These bouts were separated by minutes or hours. Many contests took more than 24h before a larva permanently abandoned a stem. Long duration contests between animals are highly exceptional and usually indicate struggles to control a valuable resource (see Maynard Smith 1982). In I. aurora and A. colenisonis observed contests consisted of a single bout lasting 30s-5min.

Observations on feeding X. zealandica larvae (Chapters 4, 5) indicated that three sensory modalities were used. All larval instars appeared sensitive to vibrational and tactile stimuli from prey. Later instar larvae were shown to have some form of chemoreception and, from

reactions to events outside the aquaria, vision appeared acute.

Observed displays were largely stereotyped and although variation occurred within them, the displays remained discrete. Therefore they could be classified unequivocally. Displays described here as agonistic were adopted rapidly and generally following some motion by a nearby conspecific. Except where otherwise stated these motor patterns were not seen in solitary larvae.

(Square brackets [] are used in the descriptions to cross reference behaviours)

Agonistic displays observed in both instar 6-8 and instar 12-14 X. zealandica larvae

1) Standing (Fig. 8a)

A larva was regarded as 'standing' when it stood with its body raised above the substrate and with its caudal lamellae spread to a separation of about 30-40°.

Circumstances: in 6th-8th instar larvae this posture was normal for undisturbed or lone animals. If disturbed, e.g. if the container was shaken or vibrated, the caudal lamellae were drawn together along the axis of the abdomen and the body was drawn against the substrate.

In 12th-14th instar larvae this posture was adopted (usually from the cryptic posture [17]) following the approach of conspecifics or prey or when walking across the aquarium floor.

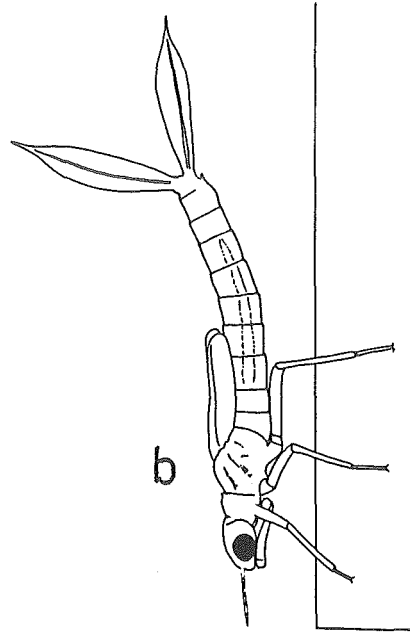
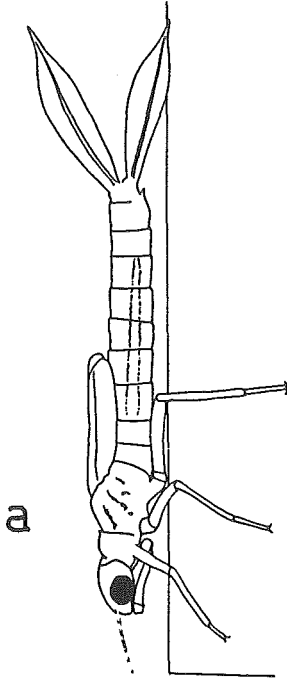
2) Abdomen raise (Fig. 8b)

In 6th-8th instar larvae the abdomen was raised through a shallow angle (about 15-20°) at the first or second segment and held in this position.

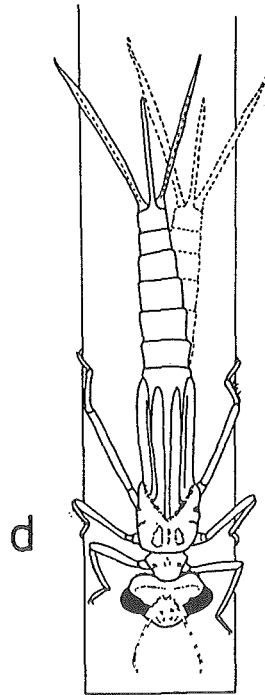
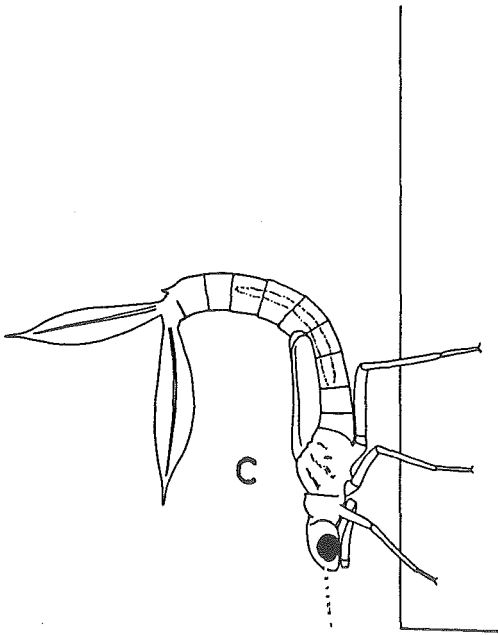
In 12th-14th instar larvae the spread of the caudal lamellae was more prominent than in younger larvae. From the standing position the larva raised the tip of the abdomen dorsally and simultaneously spread the caudal lamellae wider. The median lamella was held perpendicular to

Fig. 8. Agonistic behaviours of X. zealandica larvae I.

- a) standing posture
- b) abdomen raise
- c) lamellae forward
- d) static caudal swinging (SCS).



10mm



the substrate on which the larva was standing.

Circumstances: in 6th–8th instar larvae this display was common when other conspecific larvae approached within about 1–2 body lengths.

In 12th–14th instar larvae the posture was often adopted by occupants when a conspecific approached within 2–3 cm. It sometimes occurred when a larva was approached by animals too large to be prey or by experimenter's forceps etc. In the latter cases it was usually followed by a rapid lateral movement [9] and adoption of the cryptic posture [17].

3) Lamellae forward (Fig. 8c)

The abdomen was bent dorsally so that at the finish of the movement the caudal lamellae were spread above the head. The position is held for some seconds. In 12th–14th instar larvae this movement is very rapid.

Circumstances: in 6th–8th instar larvae seen in animals being advanced upon or lunged at [7] by conspecifics. On a few occasions it occurred following SCS [4].

In 12th–14th instar larvae it occurred in response to the approach of large animals, experimenter's finger, forceps etc. and, infrequently, in response to the close and rapid approach of a conspecific. This posture was usually followed by a rapid lateral movement [9] and adoption of the cryptic posture [17].

4) Static Caudal Swinging (SCS) (Fig. 8d)

The larva stood with all legs grasping the substrate and bent its abdomen laterally to one side and then the other. The bend occurs at the first to third segment. In very small larvae (about instars 5–6) mounting stems, the amplitude was low so the movement was barely discernible and the period was long (about 4–5s). When two animals were on the same stem the swinging had a larger amplitude (about 10°) and a shorter period (about 0.25–0.3s).

In 12th–14th instar larvae this display is highly stereotyped (Fig.

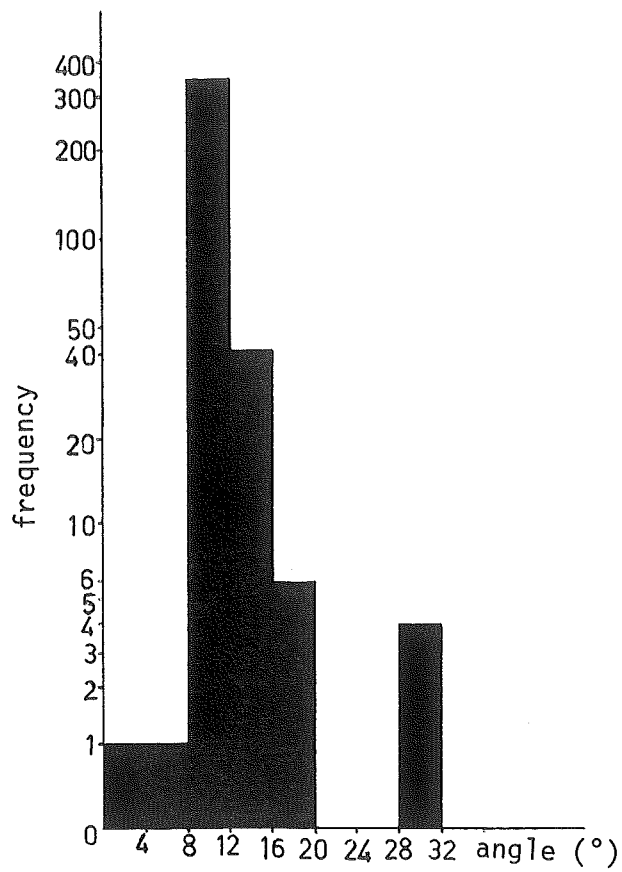


Fig. 9. Amplitudes of 405 consecutive SCS (static caudal swinging) acts. (33 acts which ended in the rest position (angle = 0°) were omitted from the analysis).

Table 3. Stereotypy of *Xanthocnemis zealandica* static caudal swinging display in terms of the stereotypy coefficient of Barlow 1977. Swings which ended in the rest position (angle = 0°) were omitted from this analysis.

Animal	Parameter observed	Mean	Stereotypy	n
A	Amplitude	11.15°	4.11	65
A	Period	0.15s	5.08	73
B	Amplitude	12.35°	4.06	80
B	Period	0.20s	4.03	80
C	Amplitude	9.93°	21.4	30
C	Period	0.16s	5.19	31
D	Amplitude	14.09°	6.48	90
D	Period	0.27s	6.83	98

9; Table 3). The straightened abdomen is bent through about 10° on each side with a period of about 0.2 s; the behaviour typically comprises bursts of 2–19 cycles (e.g. one animal – mean = 5.31, S.D. = 2.5, $n = 70$ bouts; another mean = 3.70, S.D. = 1.84, $n = 92$) separated by quiescent periods of 2–10s.

Circumstances: in 6th–8th instar larvae seen when animals were mounting stems and when two animals were close together on the same stem. In the latter case SCS was sometimes followed by lamellae forward display [3].

In 12th–14th instar larvae this display was observed under the following conditions: when larvae first occupied a perch; in vacuo on perches; when larvae were approaching (or approached by) a conspecific while on a perch (in which case the animals often alternated, only one producing SCS at any given time); when dragging carrion back to a perch (Chapter 5); following SCS by the resident of a neighbouring perch, or SCS by the occupant of a perch in an adjacent aquarium (when, in established aquaria, the animals often alternate, only one producing SCS at any given time).

5) Slow Static Caudal Swinging (Slow SCS)

The larva stood with all legs grasping the substrate and bent its abdomen laterally at about the first to fourth segment. The movement had an amplitude of about 90° and a period of about 3s. There was a slight pause at the maximum displacement before the return movement began. Typically this display is repeated for 3–5 cycles. In 8th instar larvae mounting stems the abdomen bends through about 90° with a period of about 2s.

Circumstances: in middle instar larvae this display occurred when mounting stems and when facing an opponent.

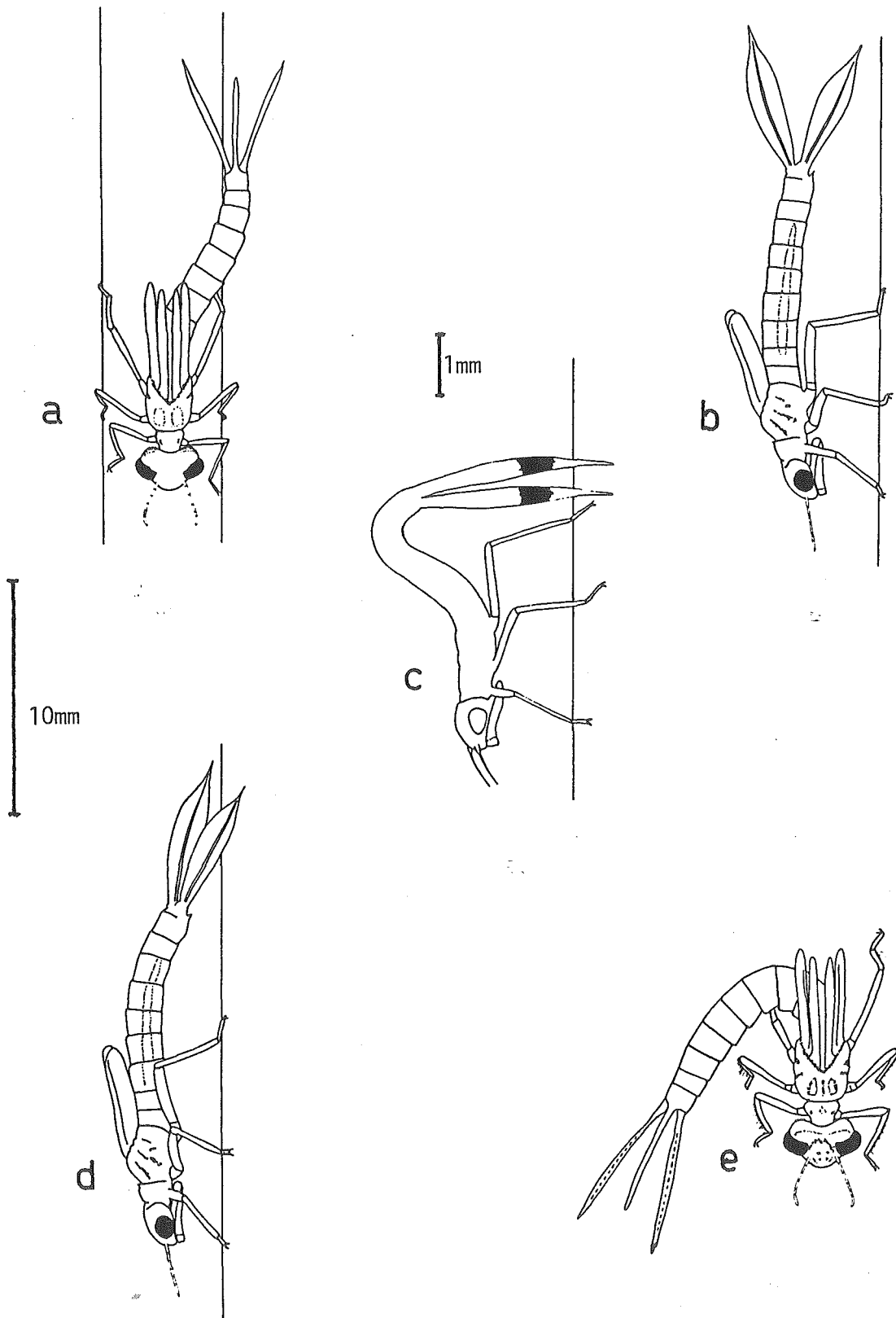
In 12th–14th instar larvae the display occurred when facing an opponent, generally after bouts of SCS.

6) 'S' bend (Fig. 10a)

The abdomen is bent laterally through about 60° at the second or third

Fig. 10. Agonistic behaviours of X. zealandica larvae II.

- a) 'S' bend (I. aurora figured)
- b) lunge
- c) abdomen arch down (6th instar)
- d) abdomen arch down (final instar)
- e) slash.



segment; and near the seventh segment there is a strong bend in the opposite direction. The caudal lamellae may end up either parallel to the thorax or, with a stronger second bend, behind the thorax.

Circumstances: usually seen following an advance by a conspecific, often followed by abdomen arch [8] and/or retreat movements. This display was common in instars 6-8 but relatively infrequent in 12th-14th instar larvae.

7) Lunge (Fig. 10b)

The thorax and abdomen were arched slightly and then the larva advanced very rapidly for 2-3 steps towards its opponent. Instar 12-14 larvae also raised and spread their wingsheaths.

Circumstances: in instars 6-8 this display usually followed a period of displaying. The larva advanced upon almost invariably retreated or abandoned the perch.

In 12th-14th instar larvae it was generally observed after bouts of alternating SCS. The animal approached retreats almost instantly and often bends its abdomen laterally. After lunging many animals proceeded to the strike display [22].

8) Abdomen arch down (Fig. 10c, 10d)

In 6th-8th instar larvae the thorax was held parallel to the substrate. The abdomen was raised at the first or second segment and then bent almost vertically down at about segment 6. The caudal lamellae were held bunched together. The posture is maintained for 5-100s.

In 12th-14th instar larvae the abdomen bends down at or near segment 4, the caudal lamellae bunch together and (usually) the tips touch the substrate. The wingsheaths are drawn close to the thorax. Circumstances: in instars 6-8 this action was often followed by some form of retreat movement or abandoning of the perch.

In 12th-14th instar larvae it occurred after bouts of SCS [4], lunge [7] and labial strike displays [22]. It was almost invariably

followed either by a backwards retreat or a movement off the stem.

9) Lateral movement

The larva moved suddenly and very rapidly sideways about the perch, taking as little as 0.04–0.10 s to move 90° – 180° about the stem.

Circumstances: in 6th–8th instar larvae this occurred almost invariably after a display by an opponent. Larvae often left the stem following a lateral movement.

In 12th–14th instar larvae this behaviour occurred as a response to potential predators (Dytiscidae, fish, forceps) and after SCS, lunge or strike by a facing opponent.

10) Slash (Fig. 10e)

The larva swung its abdomen laterally in a very rapid stroke, bending at the first, second or third segment. The bunched caudal lamellae at the end of the movement were opposite the head. They were then returned to the rest position. Instar 12–14 larvae take less than 0.05s to complete the action and return to the rest position.

Circumstances: in 6th–8th instar larvae this behaviour occurred when larvae were broadside on to a (generally smaller) conspecific. The other larva was often struck (sometimes even knocked off the substrate) and commonly abandoned its position and swam off.

Among 12th–14th instar larvae this display was frequently seen in larvae which were undergoing metamorphosis and had lost the ability to use the labium. Occurred when facing an advancing opponent and usually (but not invariably) following SCS. If the opponent was approaching from a slightly lateral angle the slash occurred on the side nearest to the opponent. On some occasions the advancing animal was struck by the caudal lamellae. Opponents cease to advance (and retreat if struck) and alternating SCS follows. Also seen used by stem occupants to drive off potential invaders larger than themselves.

11) Backup

A larva backed away from a displaying conspecific while continuing to face it (rather than the more common practice of turning and walking away).

In instars 12-14 the larva moved rapidly backwards for a few steps, away from a displaying conspecific.

Circumstances: in 12th-14th instar larvae observed following strike or slash behaviours by a nearby opponent. Most larvae turned and retreated head first.

Agonistic behaviours observed only in instars 6-8 X. zealandica

12) Abdomen bend (Fig. 11a)

The larva bent its abdomen laterally through about 90° and held this posture for about 5-10s.

Circumstances: this was the most common display when two larvae were facing head-on on a perch.

13) Semaphore (Fig. 11b)

With the abdomen held in the abdomen bend posture [12], the larva alternately spread and closed its caudal lamellae with a period of about 2s.

Circumstances: a common display when two larvae were facing head-on on a perch.

14) Caudal lamellae spread/close

With the abdomen and thorax held in a straight line the caudal lamellae are alternately spread and closed with a period of about 1-2s.

Circumstances: usually seen when larvae were facing head-on less than one body length apart.

15) 'Flick'

With the abdomen and thorax held in a straight line the caudal lamellae are suddenly spread further, then allowed to return to their rest position, the action taking about 0.1s.

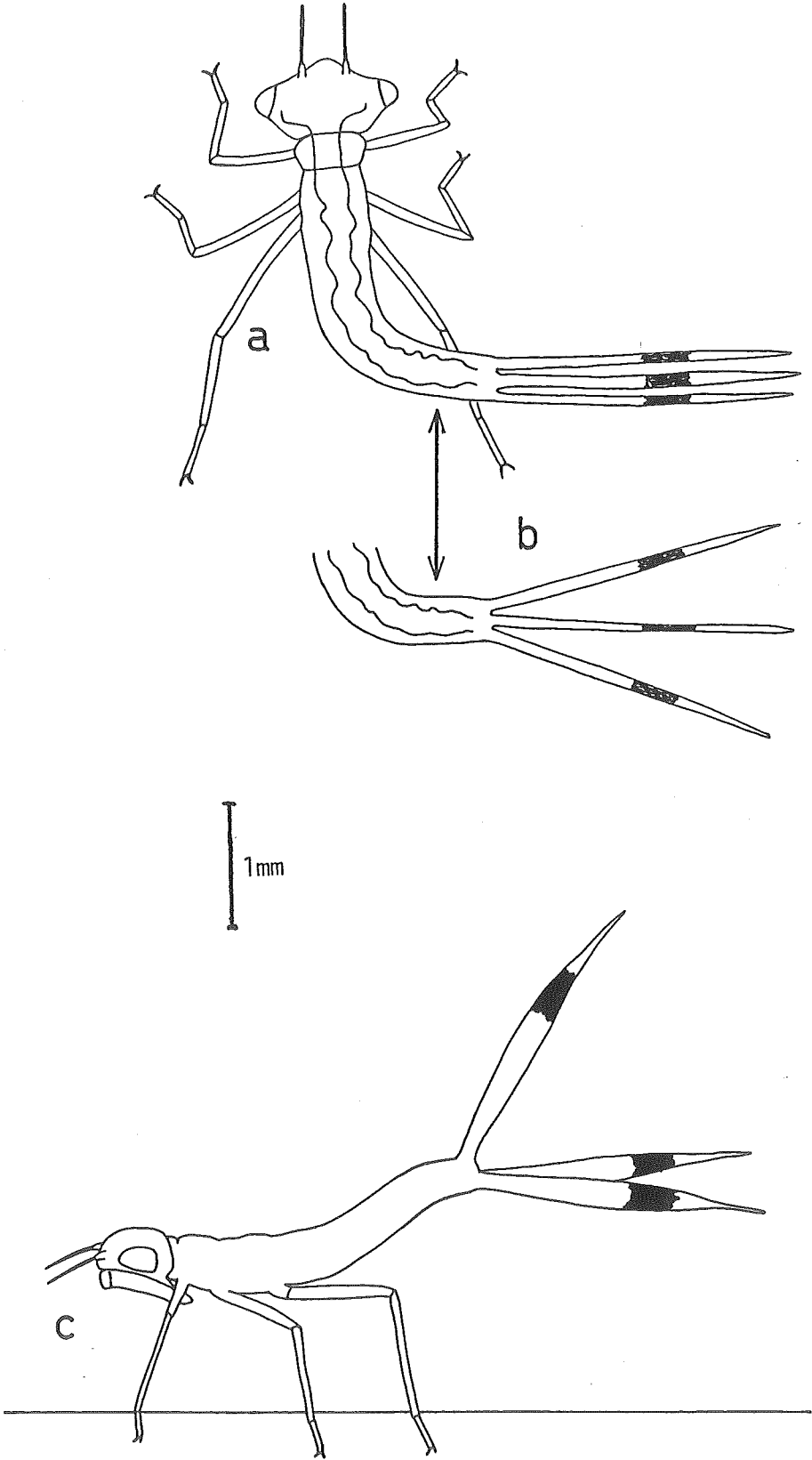
Fig. 11. Some displays apparently restricted to younger (instar 4-8)

larvae:

a) abdomen bend

b) semaphore

c) abdomen lift.



Circumstances: usually seen when larvae were facing head-on less than one body length apart.

16) Abdomen lift (Fig. 11c)

The abdomen was raised through a (shallow) angle (about 20°) at the first or second segment. At about segment 7-8 there was a distinctive kink as the abdomen tip bent to be parallel with the thorax.

Circumstances: usually seen in larvae being advanced upon by a conspecific. Often followed by a retreat on the part of the displaying animal.

Agonistic displays observed only in instar 12-14 X. zealandica

17) Cryptic posture (Fig. 12a)

The larva rested close to the perch and the caudal lamellae were held closed together.

Circumstances: this posture was normal for undisturbed residents. Larvae adopted this position at the end of a root or the base of a stem. It also occurred following lateral movement [9] in response to predators and lunge displays [7] by conspecifics.

18) Wide Static Caudal Swinging (Wide SCS) (Fig. 12b)

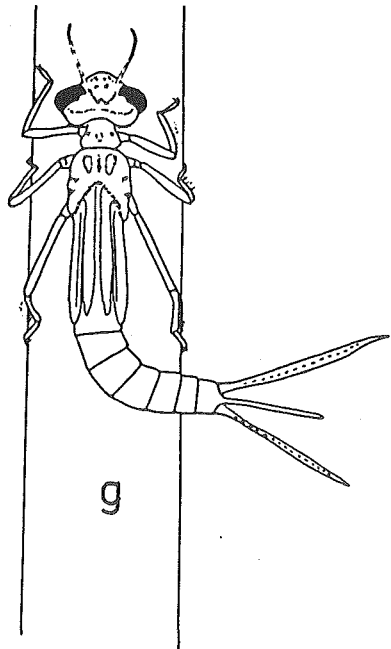
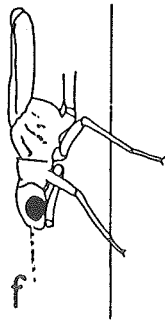
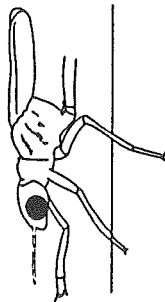
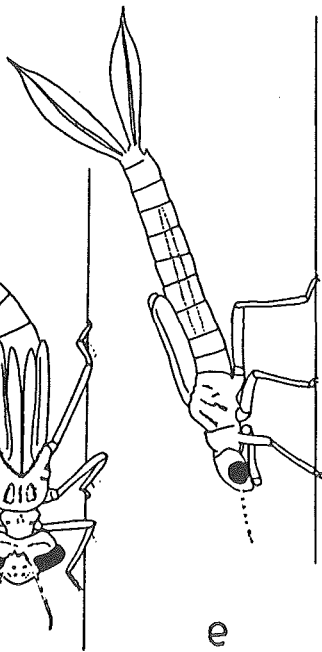
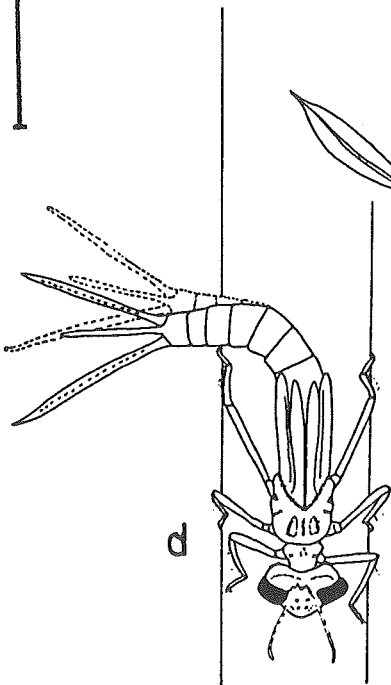
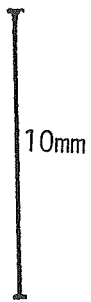
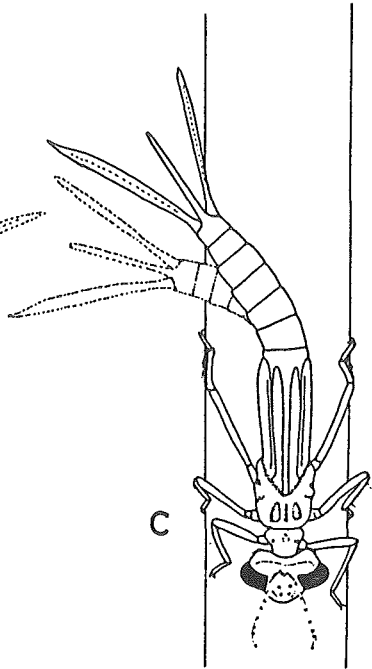
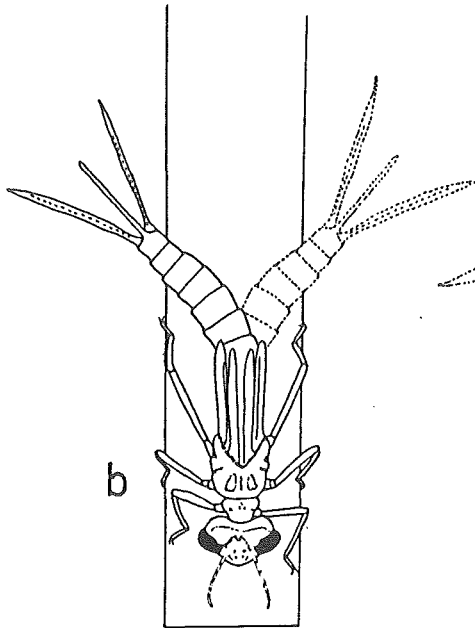
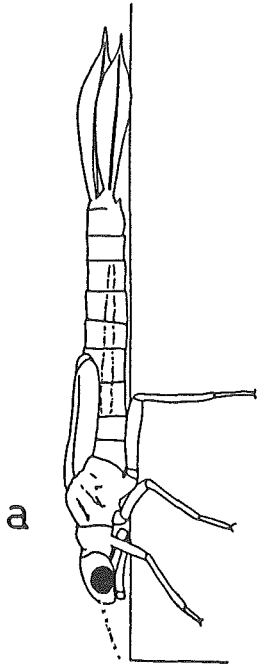
The abdomen was bent rapidly through about $30-50^\circ$, first to one side and then to the other.

Circumstances: usually observed as single or double insertions into SCS bouts. Once wide SCS appeared it usually occurred in every 2nd or 3rd SCS burst, as terminator or immediately prior to termination. Occurred either facing towards or away from a conspecific during alternating SCS and when animals on nearby stems were producing alternating bouts of SCS. This behaviour was rarely performed by solitary animals or when first occupying a stem. Prior to moulting some animals performed a display 'rumba walk' which superficially resembled continuous wide SCS, but with a period of about 1.7s. During this activity the hind legs swung in the opposite direction to the abdomen in an awkward fashion.

Fig. 12. Some displays apparently restricted to older (instar 10-)

larvae:

- a) cryptic posture
- b) wide SCS
- c) syncopated SCS
- d) abdomen bend SCS
- e) abdomen raised advance
- f) strike
- g) bend and retreat.



19) Syncopated Static Caudal Swinging (Syncopated SCS) (Fig. 12c)

The animal slowly bends its abdomen at about segment 4 to an angle of 30° (taking about 1–2s) (the 'hold' position). After a variable pause (about 1–3s) the tip of the abdomen is swung rapidly forward about 30° and back to the 'hold' position. This forward swing is often repeated. The abdomen is then moved slowly (taking about 3s) to the 'hold' position on the opposite side and the actions are repeated.

Circumstances: observed in animals undergoing metamorphosis and facing an opponent. Often occurred immediately following SCS by the opponent.

20) Abdomen bend Static Caudal Swinging (Abdomen bend SCS) (Fig. 12d)

The abdomen is bent laterally through approximately 90° and a low amplitude SCS occurs. After the SCS ceases the abdomen is straightened. The action is frequently repeated on the same side as the original display.

Circumstances: observed when animals metamorphosing prior to emergence were facing an opponent.

21) Abdomen raised advance (Fig. 12e)

The animal raised its thorax and abdomen so that they made an angle of about $20\text{--}25^\circ$ to the substrate and spread its caudal lamellae. It then moved slowly forwards (mm/s), often pausing for 30s–1min.

Circumstances: observed most frequently when animals on the aquarium floor were approaching a stem occupied by a conspecific in the standing [1], or lamellae raised [2] posture or using SCS [4]. Sometimes given by new arrivals approaching a larva on a stem.

22) Strike (Fig. 12f)

This resembled the predatory strike but (usually) occurred at too great a distance to allow contact. Frequently strikes were repeated several times in rapid succession, but on other occasions animals stood apart and struck alternately at each other. Animals which had been kept in close confinement and were then released into a large tank readily struck at

each other when close enough to grasp. In all observed cases no attempt was made to bring the caught animal to the mandibles and it was released almost instantly.

Circumstances: generally occurred at a separation of about 0.25–1 body length and after bouts of SCS (including wide SCS) or after a lunge [7]. The opponent may be facing towards or away from the striking animal. This display was usually followed by SCS (including wide SCS) by the opponent, strike by the opponent or abdomen bend retreat [23] by one of the animals. Once an animal started a strike display it often continued for some minutes after its opponent retreated or abandoned the perch.

23) Bend and retreat (Fig. 12g)

Larvae performing 'bend and retreat' turn through 180° and bend the abdomen laterally through a right angle. This posture is maintained for 30s–2min as they walk slowly away from a conspecific.

Circumstances: this behaviour occurred at the end of intraspecific displays. Most commonly it followed a labial strike display [22] by one animal or the other (i.e. after performing a labial strike an animal may bend its abdomen and retreat without any visible movement on the part of the animal struck at). After retreating 5–10cm animals often turned and again faced the opponent, or abandoned the stem.

24) Face away

The animal climbed to the top of the stem and faced the water surface (animals alone on stems moved to the bottom and faced the substrate).

Circumstances: larvae that had been occupants of stems displayed this behaviour when invaded by larvae 1–2 instars larger. Larvae adopting this posture were not seen to move down the stem to challenge the invader, but remained quiescent at the top of the stem (often for some days) until the intruder left or the smaller larva moulted.

25) Grapple

Larvae stood alongside one another (head-head or head-tail) and grappled with their legs, usually both larvae lost their hold on the substrate and fell to the aquarium floor.

Circumstances: grappling was rarely seen, and occurred only when larvae were passing each other on stems etc. On most occasions other displays occurred before the animals were broadside on. This behaviour is not to be confused with the mutual clasping of larvae when no perches are available.

Other agonistic behaviour - 'Staring'

In addition to the active displays described above, larvae may spend long periods facing each other at close range. While 'staring' larvae are unresponsive to any but the strongest stimuli (e.g. interference by the experimenter), stimuli such as contact with prey items and wandering conspecifics rarely had any effect during 'staring'.

Agonistic displays at night

Bouts at night differed from those observed in daylight. SCS was less frequent and generally of short duration and in many contests it was not observed at all. Some larvae which used SCS in the initial stages of a bout were defeated and abandoned the stem, even though they had advanced on their stationary opponent. During the contests the larvae faced each other and approached more closely than in daylight. In all cases observed, the antennae overlapped, and in some cases antennae may have been in contact with the head of the opponent. Almost all (9/11) contests were terminated by strike displays. Unlike contests in daylight the opponent was struck in these displays, but no attempt to grasp or hold was seen.

Contests in habitats where visibility is restricted (e.g. in turbid water) probably resemble those observed at night.

Onset of agonistic behaviour*

Because systematic observation of very small larvae was impracticable, the age at which agonistic displays first occur was not determined. There is evidence that some agonistic interactions occur in all instars as 2nd instar larvae were seen to slash display [10] at conspecifics. When several young larvae were kept in one container mortality was high. Fourth instar larvae were videotaped making the abdomen bend [12] display at 6th instar larvae.

Agonistic displays observed in final and penultimate instar I. aurora

Larvae of I. aurora did not adopt a cryptic posture similar to that shown by X. zealandica, but instead spent almost all their time standing. Two forms of SCS were observed. The first resembled SCS of X. zealandica [4], except that the amplitude was relatively much lower (bending $< 5^\circ$ on each side) and the period of the action was much shorter ($< \text{about } 0.1\text{s}$). The second form had the amplitude and general facies of the slow SCS in X. zealandica [5].

Circumstances: SCS type actions were observed only when larvae are close (and generally facing), not when larvae were alone on stems.

A display similar to the 'S' bend display of X. zealandica was observed at the end of one bout of slow, alternating SCS. The opponent immediately abandoned the stem.

Rapid lateral movement [9], backup [11], abdomen raised advance [21], abdomen bend and retreat [23] and grapple [25] occur in I. aurora. They appear indistinguishable from the behaviours of X. zealandica.

The strike display [22] occurred much closer to another larva than was seen in X. zealandica. Opponents frequently were grasped and the

* since the publication of this chapter (N.Z. J. Zool. 12: 1-15) abdomen bend [12] has been observed in second instar X. zealandica larvae.

attacking larva attempted to draw the opponent back to its mandibles. Attacked larvae struggled to free themselves. No obvious difference from the predatory strike was apparent.

Display observed in late instar A. colenisonis

Only a single display, utilising a different motor pattern from that occurring in the Coenagrionidae was observed in A. colenisonis. The body is lifted and the abdomen raised over a period of about 0.2s, and then dragged convulsively towards the substrate. After a pause of 1-2s the action is repeated. The cycle is repeated 10-20 times before the larva pauses. During this display the wingsheaths are extended from the body and spread. The body movement is effected by the second and third pairs of legs. When a larva is displaying on a smooth surface the body is raised, then remains stationary as the legs jerk up.

Circumstances: Observed in larvae perched on macrophytes and on the aquarium floor. Also observed in larvae standing on the bottom of shallow ponds. When one animal started making this characteristic movement many other nearby larvae also began to display the behaviour (both in the aquarium and in the field).

A. colenisonis larvae frequently strike at, and grasp, the legs of conspecifics. Attacked larvae usually 'corkscrew' free, but occasionally autotomise the leg.

Specificity of displays

In an attempt to discover features used to 'recognise' conspecifics X. zealandica larvae were exposed to contact with a variety of other, similar sized, aquatic insects. As previously reported (Rowe 1980), Trichoptera (Olinga feredayi (Coenesucidae) and Triplectides sp. (Leptoceridae)) and Ephemeroptera (Deleatidium sp. (Leptophlebiidae)) larvae were largely ignored, and did not induce predatory responses or threat displays. When X. zealandica larvae in the last four larval

instars were presented with Deleatidium larvae of about half their own length predatory responses occurred in contrast to the agonistic display responses to conspecifics with a similar size disparity. The only agonistic response to Zelandoperla sp. (Plecoptera: Gripopterygidae) was a solitary instance of strike display at an animal the X. zealandica was following down a stem. In the laboratory, close approaches by similar sized A. colenisonis larvae often induced SCS displays in X. zealandica, especially when both larvae were on the same stem. X. zealandica larvae were not observed to trigger display by the A. colenisonis. Features by which X. zealandica larvae recognise zygopteran larvae would seem to be highly specific.

DISCUSSION

Signals

In any biological communication system, signal complexity is limited by the physical properties of the intervening medium, the (spatial and temporal) resolving power of the receptor organs, the ability of the animal's nervous system to discriminate between signals and the occurrence of suitable motor patterns within the behaviour of the species to provide the evolutionary precursors (Darwin 1872, Tinbergen 1951) to signals.

It is unlikely that chemical communication plays any part in intraspecific agonistic interactions in these species. X. zealandica larvae are known to respond to chemical gradients when scavenging but diffusion through the water mass is relatively slow, highly unpredictable and, especially in a lotic situation, concentrated in the direction of any currents. Furthermore, chemical signals are persistent and therefore lack flexibility as signals during agonistic encounters (Marler 1977).

Dragonfly larvae are known to be sensitive to waterborne vibrations (Corbet 1962), and aquatic insects, such as larval Hydropsychidae

(Trichoptera) (Jansson & Vuoristo 1979), and Epiophlebia superstes (Odonata: Anisozygoptera) (Asahina 1950, Corbet 1962) produce sounds during agonistic interactions. Acoustic and displacement wave communication appear to be preadapted for use during agonistic interactions; the location of the transmitter can easily be ascertained, and changes in signal transmission can be effected rapidly. The physical dimensions of young larvae makes the generation of sound or displacement waves improbable and no specialised sound production organs are known in the zygopteran larvae investigated here.

Optical signals allow easy localisation of the signaller and can be varied rapidly. However, in a freshwater environment vision may be restricted by low light intensities or water turbidity. In contrast to acoustic signals, potential recipients (both conspecifics and predators) of optical signals can, in general, be detected by the signaller.

In very young instars of the species examined here vision is limited and consequently optical signals are probably unimportant. Second instar X. zealandica larvae have seven ommatidia in each compound eye and there can be little form discrimination. The number of ommatidia increases rapidly: third instar larvae have 12 ommatidia in each compound eye; fourth, 28; fifth, about 88 and sixth, more than 200. Fourth instar larvae respond to prey 1.3mm (one body length) away and sixth instar larvae have a dorsal pseudopupil covering 9 ommatidia, indicating a specialised eye (Horridge, 1978). The time of appearance of a dark spot badge on the caudal lamellae (Fig. 10c; 11a, b, c) corresponds with the development of the eye to the point when calculations show detection of such a badge by potential opponents is feasible.

In later instars, vision is important in detecting intraspecific displays. Larvae often begin SCS apparently in response to a displaying animal in a nearby aquarium. In this situation communication using water vibrations or chemicals is impossible.

Vision is probably the dominant sense used in intraspecific interactions, vibrational signals (or vibrational correlates of visual signals) appear to be used under conditions where vision is restricted. Contact vibration detection or chemoreception may occur during agonistic encounters at night, as the response to contact with conspecifics differed from that observed with prey.

The stereotypy (Barlow 1977) of the X. zealandica SCS display (Table 3) is similar to that of such well known displays as the 'waving' of Fiddler crabs (Uca sp.) and the 'pushup's of lizards (Anolis nebulosis and Uta sp.) (Table 2 of Barlow 1977). The stereotypy of the amplitude of the SCS display may be overestimated because of the limited resolving power available when measuring angles from a video frame (e.g. animal 'C', Table 3); this problem did not occur when measuring period.

Signal precursors

During ritualisation (i.e. the evolution of displays) precursor behaviours become modified (for example stereotyped) in such a way that they become more effective in communication. The relatively inflexible nature of the cuticle limits the number of precursors available for the evolution of displays in arthropods. Consequently arthropod visual signals tend to consist of stereotyped and repeated motor adjustments of body parts. The limited number of precursors of this sort available for locomotion, grooming movements and so on can result in the same basic movement patterns being adapted repeatedly, and independently, for similar signalling purposes in widely disparate taxa. For example, Heymer (1970) and Rowe (unpubl. obs.) have observed larval Aeshnidae (Odonata: Anisoptera) using lateral abdominal slashes in intraspecific clashes and, despite the superficial similarity to the behaviour used by the coenagrionids, these behaviours are clearly not homologues.

Ontogeny of signals

Changes in the signals utilised are to be expected in animals such as dragonfly larvae which undergo marked changes in size, morphology and resolving power of the receptor organs (Corbet 1962). Signals matched to the acute vision of later instar X. zealandica larvae would be severely degraded by, or even be undetectable to, the simpler organs present in earlier instars. Conversely, the simple, slow signals well matched to the sensory systems of early instar larvae would convey information at a rate completely mismatched to more acute senses of late instar larvae.

Between the 6th and the 12th instars of X. zealandica, changes were found both in the ritualised behaviours displayed and in the frequency of use of retained behaviours. Certain displays (semaphore, caudal lamellae open/close and abdomen lift) were observed only in instar 6-8 larvae. They may occur in older larvae, but at such low frequency that they passed unnoticed. The 'slash' was common in early instar larvae, occurred less frequently in late instar larvae, but was again common in metamorphosed larvae (i.e. pharate adults). This may be because small larvae receive more limited sensory information about their opponents and the 'slash' is a generally effective defence. Larger larvae with their more highly developed sensory apparatus use more specific ploys. Pharate adults are unable to strike at opponents because of physiological changes; therefore the 'slash' is probably their only available defence. Changes occurred in the form of SCS, abdomen arch and abdomen bend, the last gaining a caudal swinging component. Abdomen bend changed from being the most commonly observed display to becoming rare, and was also modified. 'S' bend was common in earlier instars, but occurred very infrequently in late instar larvae. SCS which occurred infrequently in the earlier instars (and was highly variable in both period and amplitude) was stereotyped (Fig. 9) and the most commonly observed display in older larvae. At least three behaviours are gained in

the later instars: cryptic, bend and retreat, and SCS variants.

During ontogeny, the shape of the caudal lamellae of Zygoptera larvae (and hence their potential for use in signals) changes markedly (e.g. Tillyard 1917, MacNeill 1960, Pilon & Masseau 1983). At the moult to the 4th or the 5th instar the narrow lamellae of young larvae develop a prominent, dark pigmented, sub-apical patch (or 'badge'), formed by a granular, subcutaneous pigment which can escape through wounds. In X. zealandica the size of the badge varies somewhat between larvae. Typically the length is about 10% of the total body length (i.e. 15% of the body length without caudal lamellae) and its area is about 30% of the cross sectional area of the larva. Similar badges have been recorded in many larval Coenagrionidae (MacNeill 1960). The visibility of the caudal lamellae is enhanced during displays by the dark contrasting markings of the badges. To an opponent these would appear as large as their head-on view of the displaying larva (markings are very conspicuous in degraded, out of focus images of SCS on videotape records). Whether the long setae on the dorsal and ventral edges of the caudal lamellae have any function in displays is unknown. Larvae (from instars 2 to 10) were never observed to respond to prey contacting these setae. However, larvae responded rapidly to strike displays directed at the caudal lamellae.

Comparison of X. zealandica with I. aurora

I. aurora was found to have a less extensive, and less ritualised, repertoire of displays than X. zealandica. This was marked by the brevity of the displays seen and the seemingly unritualised nature of the strike display, which closely resembled prey capture strikes. The displays did, however, involve similar motor patterns to those of X. zealandica.

X. zealandica appears to have either a univoltine (Crumpton 1979, Rowe in press), semivoltine, or even longer, life cycle (Deacon 1979), depending on the larval habitat. I. aurora, on the other hand, is

multivoltine (O'Farrell 1970, Rowe in press). Through much of the species' range the larvae of I. aurora utilise temporary habitats. They appear to have special adaptations to such habitats, e.g. the first few larval instars require a relatively high temperature to survive, growth is rapid, the larva moves about a lot and at about 20°C the final instar is reached within 140 days of oviposition (Rowe in press). Animals utilising ephemeral habitats (as I. aurora appears to do) must be capable of completing development within a stringent time constraint. They can, therefore, be expected to be more active hunters than the cryptic 'sit and wait' predator larvae of X. zealandica and, as a consequence, be under little pressure to evolve site defence displays. In the North Island of New Zealand both species are common in the weed zone of permanent ponds; they may, however, occupy slightly different habitats (Rowe in press).

Other coenagrionid larvae

Baker (1981a) investigated the agonistic behaviour of Coenagrion resolutum (Hagen), a species ecologically closer to X. zealandica than I. aurora (Baker & Clifford 1981). Baker's methodology involved introducing two animals to a container and allowing them to settle for 5 min before removing a partition between them and observing any interaction. For reasons discussed in the introduction to this chapter, this method was not considered suitable for examining the behaviours of X. zealandica. Therefore the results of Baker's work and those reported here cannot be compared directly. However, many of the motor patterns observed in the two studies do appear to be similar, differing largely in the details of the display (amplitude, period).

Attempts to assign precursors to displays must be somewhat speculative (but see Hailman 1977). The SCS displays of coenagrionid larvae involve similar motor patterns to those used by members of this

family in swimming. The main differences are that the animal retains a grip on the substrate and, except in 'rhumba walk' wide SCS, there is no thoracic counter movement as occurs when swimming. The rate of movement of the caudal lamellae through the water is lower, the amplitude of the stroke is reduced and stereotyped, and the angle is not the same as when used for propulsion. The abdomen arch display of young larvae is very similar to the movements used when grooming the caudal lamellae. The main differences are that when cleaning, the abdomen is drawn up (as in the display), and the metathoracic tibiae and tarsi rub repeatedly down the lamellae before the animal returns quickly to the standing posture. When displaying there is no movement of the metathoracic legs and the posture is held for some time. In older larvae while grooming movements very closely resemble those utilised by younger larvae, little of the assumed precursor remains in the display. The abdomen is bent slightly and the lamellae are drawn together. The context, however, remains the same. Thus in older larvae the abdomen arch display appears as the antithesis of the lunge, SCS and lamellae raising displays. During its ontogeny the display passes through a phase during which it is every bit as conspicuous and as prone to increase the apparent size of the animal as the aggressive displays. Some larvae repeatedly cleaned their caudal lamellae during breaks in display bouts. This, interpreted as a displacement activity, could provide the association between precursor and agonistic behaviour. The lamellae forward display closely resembles the 'parachute' posture adopted by larvae falling through the water column. When 'parachuting', larvae arch their abdomen dorsally, spread the caudal lamellae and make a stable descent with their legs and feet spread to grasp the bottom on touchdown. The strike display obviously is derived from the predatory strike. In I. aurora it still closely resembles a predatory attack, however in X. zealandica it has become highly ritualised with respect to the distance at which it is used (at least when vision is effective)

and in the absence of the grasping and dragging back components of the predatory behaviour.

Potential precursors of the abdomen bend, caudal lamellae spreading and abdomen raising displays, or of the posture during the lunge display, are not apparent. To some extent these displays all resemble comfort movements adapted to increase the apparent size or conspicuousness of the displaying animal. Modifications which increase the apparent size are common during the ritualisation of agonistic displays (Eibl-Eibesfeldt 1970).

No obvious precursor could be found for the sole display observed in A. colenisonis. The motor pattern did not resemble any observed locomotory or comfort movement. Escape movements in A. colenisonis differ markedly from those seen in the coenagrionid larvae. While the coenagrionid larvae rely on crypsis, A. colenisonis larvae, when disturbed, swim off rapidly with their legs pressed close to the body, and burrow into bottom sediments. A. colenisonis is a highly mobile, fast growing predator which, when disturbed, flees rather than hides. The absence of a repertoire of stereotyped agonistic behaviours is consistent with the apparent unimportance of fixed sites in its lifehistory tactics.

Alternating signals

Bouts between coenagrionids where opponents alternate in presenting SCS and strikes are similar in form to the well known phenomenon of 'countersinging' in territorial birds (Armstrong 1973), perhaps indicating some comparable limitation on the signalling. It is possible that many animal signalling systems are unable to operate simultaneously, but instead must 'time-share' the available communication channel. Mechanisms that would produce such a limitation might include the inability to transmit and receive data simultaneously (through either neural system limitation or 'cross-talk' between transmitted and received

signals) and the loss of sensor sensitivity through the generation of 'noise' while signalling.

Communication and 'cheats'

There has been considerable interest among theoretical biologists over the capacity of 'cheats' (phenotypes which 'bluff' intention or resource holding potential) to infiltrate into animal signalling systems (Krebs & Davies 1978, Maynard Smith 1982). In X. zealandica many of the displays (SCS, strike etc.) would seem to be good indicators of body size and general physiological state and therefore reflect fighting ability. It would appear difficult for a 'cheat' display to infiltrate the repertoire. So long as the display is not entirely ritualised, animals which 'bluff' are likely to be exposed to escalated conflicts with animals that possess the attributes being counterfeited. Such escalated conflicts should be highly disadvantageous to the weaker (i.e. bluffing) animal. In display situations, animals are probably not attempting to transmit information so much as to glean it. It would be highly adaptive for an animal to be able to 'read its opponent', thereby reducing risk to itself. Displaying may be a cost paid to gain this information. A mistake by an opponent which causes it to overestimate its prospects will be its problem! Real fights always involve asymmetries and determining the nature of these asymmetries prior to any potential escalated conflict would be advantageous to each protagonist. It is easy to imagine that animals could evolve mechanisms which allow them to evaluate their own capabilities relative to those of the general population (i.e. to play against the field). An apt analogy for these kinds of conflicts perhaps can be found in the card game poker, rather than in bridge or in the 'stones, scissors, paper' of game theory analysts.

The 'message' in all agonistic displays is probably a variant on 'I am dangerous, I want to be left alone' (with the recipient left to evaluate what 'I' is). Thus, given general limitations on display

Table 4. Agonistic repertoires from various studies (n, number of displays)

taxon	Agonistic displays	<u>n</u>	authority/comment
dragonfly larva <u>Xanthocnemis</u>	25	-	ontogenetic changes incorporated
Cockroach <u>Nauphoeta cinerea</u>	17 (11 categories)	-	Bell & Gorton (1978)
Wolf spider <u>Schizocosa</u> sp.	20 acts 9displays	-	Aspey (1977)
Fiddler crab <u>Uca pugnax</u>	11	-	Hyatt & Salmon (1978)
<u>U. pugilator</u>	9	-	Hyatt & Salmon (1978)
<u>U. rapax</u>	21 (15 ritualised)	-	Crane (interpreted by Hyatt & Salmon)
blue crab <u>Callinectes</u>	9	-	Jachowski (1974)
Hermit crabs	15	-	Hazlett & Estabrook (1974)
Palaemonidae <u>Macrobrachium</u> <u>australiense</u>	14	-	Lee & Fielder (1983)
Shrew <u>Blarina brevicauda</u>	11	54	Martin (1980)
Seal, Northern elephant male	16	-	Sandegren (1976)
<u>Mirounga occidentalis</u>			

repertoire size, it should be expected that agonistic display repertoire size will be approximately constant (in contrast to courtship and ecologically determined displays). This expectation seems borne out in a brief literature survey (see Table 4).

Phylogeny and the evolution of displays

Comparative studies of modal action patterns (Barlow 1977) have proved useful in elucidating patterns of phylogeny and ritualisation of displays (e.g. Heinroth 1911, Lorenz 1941). The first appearance of the Coenagrionidae in the fossil record is in the early Cretaceous (< 129 MYBP) (Jarzembowski 1984). The Coenagrionidae contains some 1250 species in 95 genera (Davies 1981). Most work on ritualisation has been concentrated on mating displays which might be expected to be conservative and saltational (Lambert & Paterson 1982). In contrast, the agonistic displays of larval Coenagrionidae are not confounded by courtship, aggression inhibition towards mates, or the stabilising effects of intersexual selection. Should larval agonistic displays be widespread within the Coenagrionoidea (as suggested by the anecdotal evidence of SCS presented in the introduction), the potential is present to examine phylogenetic changes and ritualisation in a very diverse group. The variety present in the repertoire of X. zealandica indicates that the signalling system is sufficiently rich to permit fruitful analysis. At first glance the number of displays observed may appear unexpectedly large. While the repertoire size may be slightly inflated due to the incorporation of displays found throughout the larval life, it should hardly be surprising that a predator operating in a complex and chaotic environment against a diversity of prey types also has the capacity to cope with a large signal repertoire. The pattern recognition ability implicit in the ability of X. zealandica larvae to distinguish between potential predators and large potential prey items, would be a potent preadaptation towards identifying 'conspecifics' and

distinguishing between elements of a large signal repertoire. Activities which increase occupant self-advertisement, and thereby improve site defence against conspecifics, run counter to the pressures imposed by the risk of alarming potential prey or of attracting potential predators. There would appear to be considerable adaptive advantage to the use of complex, highly specific stimuli. Complex IRMs, such as appear to be involved here, are extremely interesting. The ability to discriminate between similar objects using a suite of cues implies the existence of sophisticated signal processing in the pattern recognition portion of the CNS.

In the Coenagrionidae there exist a number of geographically isolated genera which have radiated extensively, producing phenotypes remarkably similar to ecological equivalents (in other genera or even other families) elsewhere (e.g. Nesobasis in Fiji and Megalagrion in Hawaii (Donnelly 1974)). Examination of larval threat behaviours in these genera would permit comparisons between species of known phylogeny, and ecologically and morphologically similar species (which presumably evolved under similar environmental constraints) of a markedly different phylogeny. The occurrence of species radiations of determinable age in genera such as Nesobasis, Megalagrion, etc. provides a means of testing recent conjectures (Moynihan 1970, Andersson 1980) that agonistic displays are subject to rapid turnover. The similarities in motor patterns of the X. zealandica, I. aurora and C. resolutum displays does not, at this stage, support the conjecture.

CHAPTER 3

Static Caudal Swinging and respiration in larval Xanthocnemis zealandica (Odonata: Coenagrionidae)

INTRODUCTION

The function of the caudal lamellae of zygopteran larvae has long been a source of contention. Tillyard (1917) referred to the organs as gills but noted that respiratory function had yet to be demonstrated and that larvae appeared to survive their loss with no apparent hardship. MacNeill (1960) forcefully presented the case for regarding the organs as gills and attacked suggestions of alternative use including swimming, 'parachute' descent through the water column and defence.

The extensive, obvious, tracheation in many species make respiration a plausible function and the possibility of alternative functions has been largely ignored. The consensus in the literature was summed up by Corbet (1962: p49) 'There can be little doubt, however, that they have been evolved primarily as a supplement to the other, less specialized methods of respiration which larvae have at their disposal'. Corbet (1962: p54) cautioned, however, that the findings of Robert (1958) on Lestes viridus were contrary to interpretations of ventilation and respiratory function, warned against the dangers of too rapid generalisation, and noted that the organs could serve more than one function.

A number of authors have noted regular, rhythmic abdominal movements in larval Coenagrionoidea (Copera (Platycnemidae), Lieftinck (1940); Ceriagrion (Coenagrionidae), Gardner (1956); Pyrrhosoma nymphula (Sulzer) (Coenagrionidae), Lawton (1971a); Ischnura (Coenagrionidae), Thompson (1978a); Coenagrion (Coenagrionidae), Baker (1981)) and have interpreted them as ventilatory movements (Lawton 1971a:

p412, Thompson 1978b; Baker 1981a: p356). The lifting of the abdomen observed in Pyrrhosoma, Platycnemis and Isosticta (Isostictidae) (Corbet 1962) was interpreted as a movement to increase respiratory opportunity by raising the caudal lamellae clear of surrounding detritus.

Regular rhythmical movements are widely recognised as a characteristic feature of animal displays (Lorenz 1967) and Rowe (1980) regarded the regular abdominal movements of Xanthocnemis zealandica (McLachlan) larvae as a major component of the intraspecific agonistic display repertoire, a view extended in Chapter 2. Because of the widespread view that caudal movements in damselfly larvae are solely ventilatory in function, attempts were made to induce the most commonly observed agonistic display in larval Xanthocnemis zealandica 'Static Caudal Swinging' (SCS) (Rowe 1980; Chapter 2) by placing larvae under respiratory stress. A larva performing SCS repeatedly swings its abdomen laterally through 10–15° at a rate of 5 Hz and this looks superficially as if it should be a respiratory or ventilatory behaviour.

METHOD

Conical flasks (2l) were filled to their narrow necks with water which had been deoxygenated by boiling and then cooled to room temperature. A bung with a long inlet penetrating below the water surface and a short outlet tube above the water surface (a modification of the apparatus illustrated in Popham 1954) was inserted in the neck and the water in the flasks was bubbled vigorously with oxygen-free nitrogen (New Zealand Industrial Gases).

Conical flasks were chosen because of the small surface area exposed above the water, the large area on which larvae could perch or rest and the absence of sites resembling preferred territorial sites (Chapter 8) on the concave surfaces of the container.

Oxygen content was monitored intermittently while bubbling and during the experimental period using a Yellow Springs Instruments model 54 oxygen meter. By varying the duration of nitrogen bubbling it was possible to alter the oxygen concentration in different flasks. Oxygen concentration was found to increase slightly through the experimental period. This was probably due to mixing and diffusion when probes were placed into the flask.

Experiments were conducted with 1 larva/flask so agonistic behaviours would not be expressed. Unless otherwise stated all larvae were in the final instar (and not in metamorphosis). Larval activity was examined every few minutes. Larvae which appeared moribund were stimulated, either by swirling the flask to create currents or, if this was ineffective, by moving the larva about with a probe.

RESULTS

On introduction to a flask most larvae made a controlled descent to the vessel floor in the 'parachute' posture (Chapter 2) but some actively swam down.

The first experiments were conducted at an oxygen concentration of $1-1.5 \text{ g.m}^{-3}$ and between $16-18^{\circ}\text{C}$.

Larva 1:

For the first 75-90 min the larva made short walking and swimming movements. From 90-135 min the larva began to 'rest' with its abdomen and thorax arched dorsally and its forelegs raised from the substrate (Fig. 13). It responded to mild stimulation with a probe by attempting to walk or swim away from the irritant. Coordination deteriorated through this period. After 180 min the larva became moribund and ceased to respond to stimulation.

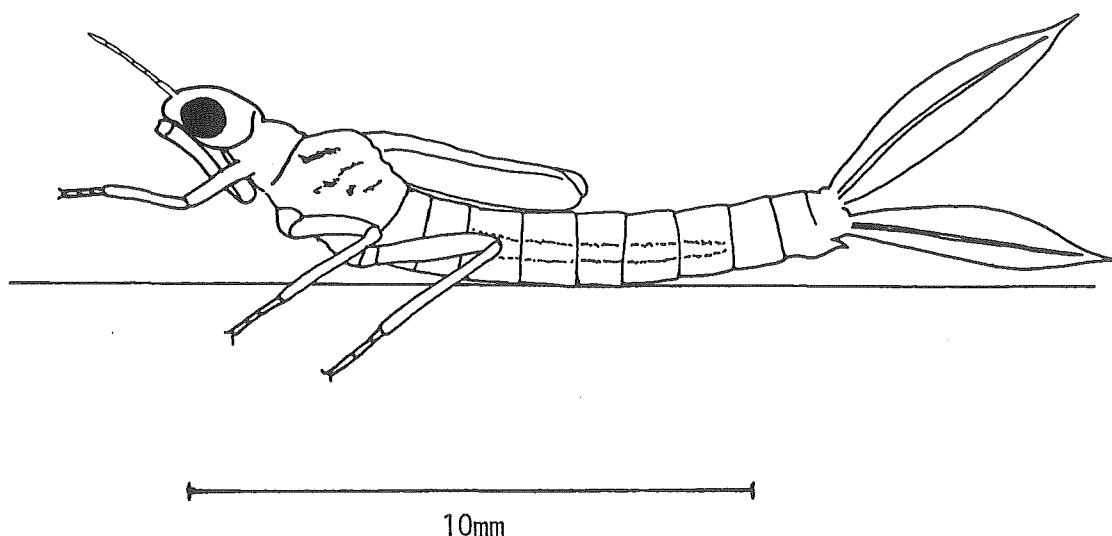


Fig. 13. Dorsally arched distress posture of X. zealandica larva under hypoxic conditions.

Larva 2:

This larva lacked caudal lamellae. About 90 min after insertion in the apparatus it was still walking and swimming when stimulated. It did not display the dorsally arched abdomen-thorax distress posture.

Larva 3:

For the first 65 min the larva walked, and occasionally swam, about. After 65 min, 2-3 SCS movements were seen, but they appeared very 'desultory'. After 210 min the larva still moved its legs in a strong and coordinated, manner when stimulated and 270 min after insertion it still moved its legs, but was unable to walk. At 330 min it attempted to swim without being stimulated. At 400 min it attempted to swim in response to stimulation.

Larva 4:

For the first 150 min the larva walked, and occasionally swam, short distances. By 210 min it had become moribund, but moved its legs in an uncoordinated fashion in response to stimulation. The oxygen concentration near the larva at this time was 0.8 g.m^{-3} . After 280 min the larva was lying on its side with its abdomen and thorax arched dorsally and it did not respond to stimulation. After 390 min the local oxygen concentration was 1.1 g.m^{-3} and the larva moved its legs when stimulated.

The second set of experiments were conducted at an oxygen concentration of $0.6\text{--}0.7 \text{ g.m}^{-3}$ and between $16\text{--}18^\circ\text{C}$.

Larvae 5,6:

After 90 min both larvae held their legs curled but walked after stimulation. After 120 min both larvae were in the dorsally arched distress position. After 150 min they were moribund and by 180 min after insertion had ceased to respond to stimulation.

Larva 7:

This larva, in the penultimate instar ceased to move voluntarily 60 min after introduction. It attempted to swim after stimulation 90 min after insertion. By 120 min after insertion it was lying on its back in the dorsally arched distress position, moving its legs feebly.

Larva 8:

This larva, in the antepenultimate instar was lying on its side in the dorsally arched distress position 90 min after insertion. After 120 min it was moribund.

In a further experiment (also conducted at $16\text{--}18^\circ\text{C}$) six larvae were subjected to very low oxygen concentrations ($< 0.5 \text{ g.m}^{-3}$). Over a period of about 60 min they all became moribund and adopted the dorsally arched distress posture. Shortly afterwards they ceased to respond to

stimulation. Neither SCS nor concerted attempts to swim or climb to the surface were observed in any of these larvae.

Larvae which had been unresponsive to stimulation for some time (at least 15 minutes) recovered and resumed normal activity within 30 minutes of being transferred to water with an oxygen concentration about 9 g.m^{-3} .

DISCUSSION

Given the extensive tracheation of caudal lamellae in the older larvae of many species of Zygoptera, arguments involving respiratory function have immediate appeal and superficially appear persuasive. However, the experimental basis for this belief is not strong and evidence comes from only a few sources. Pennak and McColl (1944) found that in Enallagma (Coenagrionidae) the cuticle of the caudal lamellae was a more efficient surface for oxygen uptake than that of the rest of the body. Harnisch (1958) found in Coenagrion (Coenagrionidae) that 60% of the total oxygen uptake was through the caudal lamellae. The behaviour of Calopteryx (Calopterygidae) species at low oxygen tensions was examined by Zahner (1959) who found an elaborate sequence of responses when the oxygen tension was lowered. The larvae spread the lamellae and wing-sheaths and shake themselves from side to side; they then move to the surface and hold the dorsal surface of the body and caudal lamellae against the air-water interface. Larvae lacking caudal lamellae lift the tip of the abdomen through the surface film. Some larvae even emerge from the water.

Calopteryx species were an unfortunate choice on which to base generalisations of respiratory function. Larvae of this genus have relatively small triquetral caudal lamellae and occupy specialised habitats in running water (Zahner 1959). Many species occur only in the

current of swift, clear waters and would, if anything, be subjected normally to hyperoxic conditions (Heymer 1973). In general, species occupying flowing water habitats might be expected to be particularly sensitive to low oxygen concentrations and to lack adaptive responses to hypoxic conditions.

Piers Allbrook (pers. comm. in lit. to Corbet 1976) found Austrolestes annulosus (Selys) exhibited 'normal' respiration rates in a Gilson respirometer with 0, 1, 2 or 3 caudal lamellae and the rectum sealed to close the rectal pads which had been postulated to have respiratory function. This is consistent with the earlier findings of Robert (1958) on young Lestes viridus.

The experimental evidence on species in the Coenagrionidae indicates a low basal metabolic rate and a correspondingly small demand for oxygen. Lawton (1971a) kept P. nymphula in a variety of respirometers and found a very low oxygen demand (ca $2.5 \mu\text{l O}_2/\text{h}$ for a 0.02g wet weight larva at 20°C). This value is about 5% of the equivalent 'standard inactive poikilotherm' rate as established by Robinson et al (1983). Klekowski and Kamler (1968) showed that in Pyrrhosoma, the respiratory rate fell with a decrease in oxygen tension. Gaufin et al (1974) examined medium and long term survival of various aquatic insect species in stream tanks under controlled oxygen levels. The insects most resistant to low oxygen tension proved to be the two coenagrionids tested. Argia vivida Hagen survived at oxygen concentrations between 1.7 and 3 g.m^{-3} (50% survival after 56 days at 3 g.m^{-3} , 10% survival after 100 days at 1.7 g.m^{-3}), while Enallagma anna Williamson was able to tolerate oxygen concentrations in the region $1.1\text{--}1.4 \text{ g.m}^{-3}$ (50% survival after 21 days at 1.4 g.m^{-3} , 20% survival after 35 days at 1.1 g.m^{-3}). Deacon (pers. comm.) stated that the oxygen requirements of final instar X. zealandica larvae he tested were very low, and near the limit of the Gilson respirometer he was using. Given the low metabolic

and respiration rates found experimentally, determining the contribution of various parts of the larval anatomy as respiratory surfaces would appear technically difficult.

X. zealandica larvae usually are found at the bottom of stems, amongst dense vegetation beds and in or on detritus, all habitats with the potential for being locally hypoxic. X. zealandica larvae are remarkably hardy. If field collections become hypoxic, they are among the last survivors and under such circumstances larvae usually are found near the surface of the water or near the air bubbler. They rarely display SCS behaviour. The difference in behaviour between larvae in hypoxic buckets and in the experimental flasks where they remained more or less inactive on the bottom may be due to whatever oxygen concentration cue is used in this group. During droughts, X. zealandica larvae bury themselves in the drying mud and aestivate (Rowe in press) and they can survive many days at normal room humidity on the bare bottoms of dry containers. They would appear to have a robust respiratory physiology.

The only apparent response of X. zealandica larvae placed in low oxygen concentrations in the conical flasks was to walk across the floor. This is, however, the same response they display when placed in any new container lacking prospective territorial sites. Movement would be an adaptive response to any local lowering of oxygen tension since it provides the opportunity to locate a more appropriate environment. In a lentic situation with local environmental conditions deteriorating, remaining in position while attempting to ventilate would be a highly maladaptive response. Ventilation has its own associated respiratory cost and, under conditions of low oxygen tension, the prospect of a net benefit from the activity is doubtful.

Numerous rheophilic Ephemeroptera and Trichoptera have behaviours which enable them to pump water with a high oxygen content into dead spaces such as tubes and refuges, a highly adaptive response for an

animal inhabiting 'dead pockets' in otherwise oxygen saturated or supersaturated conditions. When placed in aquaria and subjected to non-hyperoxic conditions, these species exhibit 'ventilating' movements and obvious distress. Some have interpreted these movements as an adaptive response to an inclement environment. On the contrary, I consider these ventilatory responses represent a pathological use of a usually adaptive behaviour in an unnatural context. In an environment with low or inadequate oxygen, the additional respiratory burden imposed by ventilatory movements would accelerate the death of the animal. Unfortunately, the belief in the adaptiveness of 'ventilation' behaviour in Trichoptera and Ephemeroptera under these circumstances appears to have been transferred uncritically to (coenagrionid) Zygoptera and has meant that SCS agonistic behaviour has gone unrecognised.

When kept in still water under conditions of low oxygen tension, X. zealandica larvae remained active for at least an hour. Larvae becoming moribund adopted a characteristically arched distress position. This position was not observed under other circumstances (Chapter 2). Low oxygen tension did not induce SCS or any other behaviour recognised as being agonistic (Chapter 2).

The morphology of caudal lamellae varies greatly within the Zygoptera (Tillyard 1917, MacNeill 1960, Corbet 1962) and function might equally be expected to be as varied. In the early instars of all species the caudal lamellae are simple triquetral structures lacking extensive tracheation. During larval development the caudal lamellae undergo considerable change. In the Coenagrionidae and Lestidae they become extensively tracheated whereas in other families they retain the simple triquetral form (Calopterygidae), become bulbous and saccoid (most Amphipterygidae), weirdly sculpted (Pentaphebia, Amphipteryginae) or develop into specialised (adhesive?) organs (Diphebia (Amphipteryginae), Argiolestes (Megapodagrionidae)) (MacNeill 1960,

Corbet 1962).

The caudal lamellae are organs with considerable evolutionary plasticity. The extensive tracheation found in older larvae of many species almost certainly indicates they serve as gills but, to consider the caudal lamellae solely, or even primarily, as gills on this basis is misleading. The dark badge which appears on fourth instar coenagrionids (when the caudal lamellae lack the morphological features of a gill) and the use of the lamellae in a variety of displays by X. zealandica from about the fifth to the final instar (Chapter 2) indicates that caudal lamellae are subject to a variety of evolutionary pressures, and may be fulfilling several functions simultaneously.

Section 3: Predatory behaviour

The most detailed work on the predatory activity of larval Coenagrionidae has been carried out in England by J.H. Lawton and his students (Lawton 1970a, 1970b, 1971a, 1971b, Thompson 1978a, 1978b, 1978c, 1982, Uttley 1980). They have examined the effects of prey density and size on functional responses of damselfly larvae under standardised laboratory conditions using 100 ml pottles as the experimental universe and Daphnia magna as prey. Attempts to extend their simple experimental procedures to more complex situations (Lawton et al 1974) and larger containers (Savan 1979) met with little success. Savan (1979) found 'functional response variances were much higher in experiments conducted in large arenas' and 'attack rate and handling time probably do vary ... these variations can be masked, so that the resulting functional response curves in no way betray the violation of the assumptions on which the functional response model rests'. This led to her general conclusion that 'complexity of the predatory process is enormous; variation in most external circumstances is likely to alter the way damselflies eat. Until this process is better understood, direct application of predation theory to the field situation is unlikely to yield precise, accurate predictions'.

In addition to laboratory studies of feeding behaviour (e.g. Johnson 1973, Akre & Johnson 1979, Johnson, Akre & Crowley 1975, Crowley 1979, Baker 1980, 1981a, 1983, Lawton et al 1980 – literature review Corbet et al 1984) a large number of workers have examined the diets of coenagrionid larvae in the field. Other than in autecological studies the emphasis of ecological investigations has been on determining either the impact Zygoptera larvae have on prospective prey species or on quantifying 'niche overlap' between sympatric predatory species (Stimac & Leong 1977, Johannsson 1978, Johnson et al 1984).

Macan (1977) and Lawton et al (1980) suggested that the perches coenagrionid larvae occupied were hunting sites. If this is the case then an appreciation of both behaviours involved in predatory activity and the level of predatory activity are important prerequisites for determining the selection pressures influencing perch site selection.

There are difficulties in working with late instar (i.e. instars 10-14) Xanthocnemis zealandica in that they are cryptic, easily disturbed by the presence of an observer and have the ability to suppress predatory behaviour for long periods without ill effect. Furthermore there is some evidence that a 'learned' component within the predatory repertoire of some coenagrionid larvae (Lawton et al 1974) could confound the interpretation of investigations using larvae with an unknown history (i.e. from the field).

The predatory activities of later instar larvae proved difficult to observe because of their cryptic behaviour and their sensitivity to observer movement. These larvae are too small for predatory behaviours to be viewed readily with the naked eye or using low magnification automatic monitoring videorecording. They are intolerant of intense light which is needed for high magnification videotaping, and operator movement during filming was also found to disturb the animals. Predatory behaviour tends to be sudden and often occurs without any observed 'intention' movement. These factors made the presence of suspected predatory versatility difficult to demonstrate. Nevertheless, a number of interesting discoveries were made, including the existence of specialised scavenging behaviours. To avoid the problems involved in working with later instar larvae investigations were first carried out using second instar larvae.

In Odonata the second instar is the first feeding stage and in most species it has a very limited sensory capability compared with later instar larvae (Corbet 1962). Responses of naive second instar larvae to a variety of prey were examined to find whether prey choice or selection

occurred. Differences in response to different prey were found, although whether this was a consequence of 'filtering' through either sensory (detection) limitations or morphological constraints, or is evidence of predatory versatility remains a moot point. Some indications of learning were found when unpalatable prey were offered. Second instar larvae proved very tolerant of observer interference, in all probability because they were unable to detect the observer.

Because of the evasive behaviours of late instar Xanthocnemis larvae it was difficult to examine the predatory behaviours in any detail. An opportunity to examine a more tolerant species, Hemianax papuensis (Burmeister) (Anisoptera: Aeshnidae) was taken to demonstrate unequivocally the presence of predatory versatility in a larval odonate (Appendix 2).

Baseline data on feeding rates of X. zealandica were obtained to permit comparison of 'hunger levels' in the field and laboratory. Gut throughput time was established in the laboratory and the proportion of larvae with food in the gut at the time of collection was determined. It has been suggested (Corbet 1962: p64) that as dragonfly larvae were facultative predators information on prey composition, together with a knowledge of prey distribution would provide evidence of the actual microhabitat occupied. Faecal pellet contents were determined to supplement the work of Crumpton (1979), Stark (1981) and Dowdle (1981).

CHAPTER 4

Predatory behaviour in the dragonfly larvae Xanthocnemis zealandica -
ontogeny of predatory behaviour and predatory versatility
in young larvae.

INTRODUCTION

The predatory activities of odonate larvae have proved an attractive field for study and many investigations have been directed at ascertaining either diet or the predatory behaviours involved (reviews Corbet 1962, 1980). Despite the large size changes which occur during development of dragonfly larvae (change in linear dimensions about 15x; change in weight about 3000x) little attention has been paid to concomitant changes in predatory behaviour.

The Coenagrionidae are the most successful family in the Zygoptera in terms of both species and individual numbers (Tillyard 1926, Fraser 1957), and the ecologies of coenagrionid larvae have been investigated by many authors (e.g. Corbet 1957, Lawton 1970a, Johannsson 1978, Baker & Clifford 1981). However, the behaviours involved in predation by coenagrionid larvae do not appear to have been examined in any detail.

Odonate larvae capture prey using a rapid extension of the modified labium. In the suborder Anisoptera the rapid extension is effected hydraulically by the contraction of a muscular diaphragm in the abdomen (Corbet 1962, Pritchard 1965, Tanaka & Hisada 1980). Members of the suborder Zygoptera do not possess this diaphragm and a different, hydrodynamic, mechanism is used (Caillere 1972). In older larvae of both suborders the method of prey acquisition is essentially the same. Prey is detected at a distance either visually or through the detection of vibration. The larva orients towards the prey and, once within range,

strikes with its labium. The prey is grasped, gathered or pierced and then drawn back to the buccal cavity where it is consumed. These behavioural patterns are well coordinated and usually very fast. Prey detection and orientation may involve only a few slight movements of the head (Chapter 7) and in large Anisoptera such as the Aeshnidae the labial strike takes about 20ms (Pritchard 1965, Tanaka & Hisada 1980, Appendix 2); in Zygoptera the labial strike may be somewhat slower (0.14 – 0.25s in Calopteryx (Caillere 1965, 1974), <40ms in X. zealandica this study).

Young larvae, in the first few instars, react more slowly to the presence of prey and their prey capture motor patterns are less coordinated than those of older larvae (Richard 1961, Caillere 1974, own unpubl. obs. X. zealandica, Ischnura aurora (Brauer), Hemianax papuensis (Burmeister), Procordulia smithii (White)).

Most studies of the predatory behaviour of Odonata larvae have concentrated on species in the suborder Anisoptera (e.g. Richard 1960, 1961, Pritchard 1965). The few investigations of predatory behaviours in zygopteran larvae and comparative studies of the ontogeny of odonate predatory behaviour have, in the main, used species in the family Calopterygidae (e.g. Rease Nevin 1929, Calopteryx maculata Beauvois; Richard 1960, 1961, Calopteryx virgo (L.); Caillere 1965, 1972, 1974, Calopteryx splendens (Harris)). An exception was the study of Lawton (1970b) in which prey choice by second and third instar Pyrrhosoma nymphula (Sulzer) (Coenagrionidae) was examined. Ecological studies, in contrast to behavioural studies, have concentrated almost exclusively on species in the families Coenagrionidae and Lestidae. The Calopterygidae are a small, phylogenetically isolated group (Davies 1981, Heymer 1973) with larvae apparently adapted to and restricted to (rapid) flowing, clear water habitats (Corbet 1962, Heymer 1973).

In a typical predation sequence in C. virgo or C. splendens, prey detection is followed by the adoption of a specialised antennal posture; the larva then attempts to make antennal contact with the prey. After 'inspecting' the prospective prey with its antennae the larva strikes with its labium (Richard 1960, Caillere 1965, 1974). This behavioural sequence appears specialised and adapted to the sensorially chaotic environment presented by the flowing water habitat occupied by the larvae. With few exceptions, the predatory behaviours of other Zygoptera appear to have been ignored. Generalisations based on data gathered for Calopteryx have led to a narrow and non-representative view of zygopteran larvae as predators. For example, zygopteran larvae (other than Lestidae) generally have been regarded as non-visual predators (Corbet 1962, Thompson 1978a, Johnson & Crowley 1980) although both Pearlstone (1973) and Crowley (1979) queried this assumption insofar as the Coenagrionidae were concerned.

The youngest instar dragonfly larvae are the most sensorially limited. They are small, exhibit limited tactile responses, appear to detect vibrations only from short range and, except in the Aeshnidae (Anisoptera), their compound eyes have too few ommatidia to resolve even the simplest shapes (Ando 1957).

METHODS

Pairs of X. zealandica ovipositing in tandem were collected from a number of sites (Kaiwi Ls; L. Sarah, Cass; Waimakariri R. pond; Avon R., Christchurch; Roxburgh pond) and the females were induced to lay eggs into moist blotting paper in the laboratory (Rowe in press). Ova were maintained indoors at about 20°C until hatching occurred. Hatching batches were inspected daily and recently emerged second instar larvae removed. They were held at 20–25°C for a further 12h before experiments

were conducted (so all larvae used were 12–36h old). This holding period was introduced to ensure that larvae had successfully completed post moulting development before an experiment commenced. (After moulting into the second instar, larvae spend some time flexing and 'exercising' their labia and over the first 2–3 hours after moulting the head capsule width expands by 20–30%).

Individual larvae were introduced into a 3 cm diameter, rough bottomed, solid watchglass which contained prey organisms and a small quantity of fine plant detritus carried over with the prey culture. This detritus sometimes occurred in 'balls', and larvae tended to localise on such sites. The watchglass was observed under a stereomicroscope using darkfield illumination. A running commentary of larval behaviour was made into a taperecorder for later transcription. Observations were ended after 30 min or after a predetermined number of prey had been consumed. This cut-off level was set below the level of prey consumption at which larval behaviour began to change. Behaviour sequences were transcribed into transition arrays. (Arrays representing the frequency of behaviour dyads, the preceding behaviour determines the row and the succeeding behaviour the column to which the dyad belongs).

Six prey regimes were offered: no prey, Paramecium (sp. indet.) (at a density of about 20/25x field), bdelloid rotifers (sp. indet.), nematodes (sp. indet.) (at two densities $5.4 \pm 2.1/25x$ field and about 2/25x field), the cladoceran Alona guttata (Sars), and the harpacticoid Phyllognathopus volcanicus Barclay. The movement patterns and occurrence of local aggregations in rotifers and crustacea made estimating effective local prey density about the predator difficult. Because it was possible that changes in behaviour occurred as relative prey abundance changed and because it was difficult to replicate prey concentrations accurately from cultures with wildly fluctuating numbers, experiments were run in sequence, removing one predator and replacing it

with the next. Experimental sequences typically took 5h and involved up to 10 predators; during this time up to 50 prey animals were consumed.

Establishing the significance of transition arrays is difficult. Even testing for significant differences between cells within a single array is unsatisfactory. Fagen & Young (1978) estimate that only a third to two thirds of significant cells can be detected with current methods. Comparison between different transition arrays is even more difficult. With large (and multidimensional) arrays, Chi-square tests are prone to detect the real, but uninteresting, fact that two samples are different. In transition arrays there is a lack of independence between rows and columns and real differences propagate to all later levels in the sequence (i.e. if a column is empty then the corresponding row must also be empty and any following row for which that row is a major contributing channel will also be markedly reduced). Because of the strong off diagonal structure of the arrays, adjacent rows are often strongly coupled. Rechten & Fernald (1979) suggested that to avoid these problems of lack of independence, individual cells in behavioural transition arrays should be analysed by condensing to a 2 x 2 array with the cell of interest preserved and examining the reduced array for significance. Much information is lost if such a procedure is followed. There are major difficulties in achieving satisfactory analyses of structure (which is what is needed here). Billingsley (1961) recommends comparing rows using a Chi-square test, i.e. evaluating the distribution of exit channels from a given state, as this is robust against the existence of higher order processes.

Selected rows of arrays were compared using a Chi-square test. Rows were selected in each of the key portions of the predation sequence (viz initial response to prey, prey attack and consumption) and before comparisons were made cells with low expected frequencies were omitted (Siegel 1956). The rows selected for comparison between arrays fell at or

after different 'nodes' of the predatory process and were effectively decoupled from one another.

Some X. zealandica were raised from eggs to establish the ability of larvae to develop on the different foods used for the behavioural observations. Larvae were maintained in either 5 cm diameter Syracuse dishes or 75 x 25 mm vials and held either at room temperature (20–25°C) or in a 16 or 25°C controlled temperature room. All foods were offered separately under each environmental condition. More than 100 replicates were used for each treatment. Individual larvae were transferred to a container and an excess of food culture was added. Containers were examined weekly to determine survival.

RESULTS

Classification of behaviours in second instar larvae

Thirteen behavioural categories were recognised when preparing transition arrays:

1) Locomotion (LO)

The larva either walked across the substrate, with its body held above the floor, or swam in the water column. While walking or swimming the larva did not respond if contacted by prey.

2) Leg Spread (LS) (Fig. 14)

The larva settled and the body was lowered almost to the substrate while the legs were spread and extended. This position was maintained for long periods during which time the larvae respond rapidly to prey contact with antennae, tibiae or tarsi (Fig. 15).

3) Leg drag (LD)

A behaviour observed almost exclusively in the presence of nematodes.

Larvae in the leg spread posture (e.g. on detritus balls) suddenly dragged both hind legs forward convulsively while continuing to grip the

Predatory activity of 2nd instar X. zealandica larvae

Fig. 14. Leg spread posture

Fig. 15. Prey detection through the tactile sense. The dotted lines indicate the volume within which larvae detect prey using the tactile sense. The positions and lengths of the fine setae which are presumed to act as contact sensors are indicated. The first larval responses to harpactacoid contact with each area indicated.

(key - OB = orient body, OH = orient head, AC = antennae close, PO = palp open, ST = strike; total number of each response observed below)

Fig. 16. Orient body, response to contact with right mesotarsis figured.

Fig. 17. Behaviours involved in predation sequence:

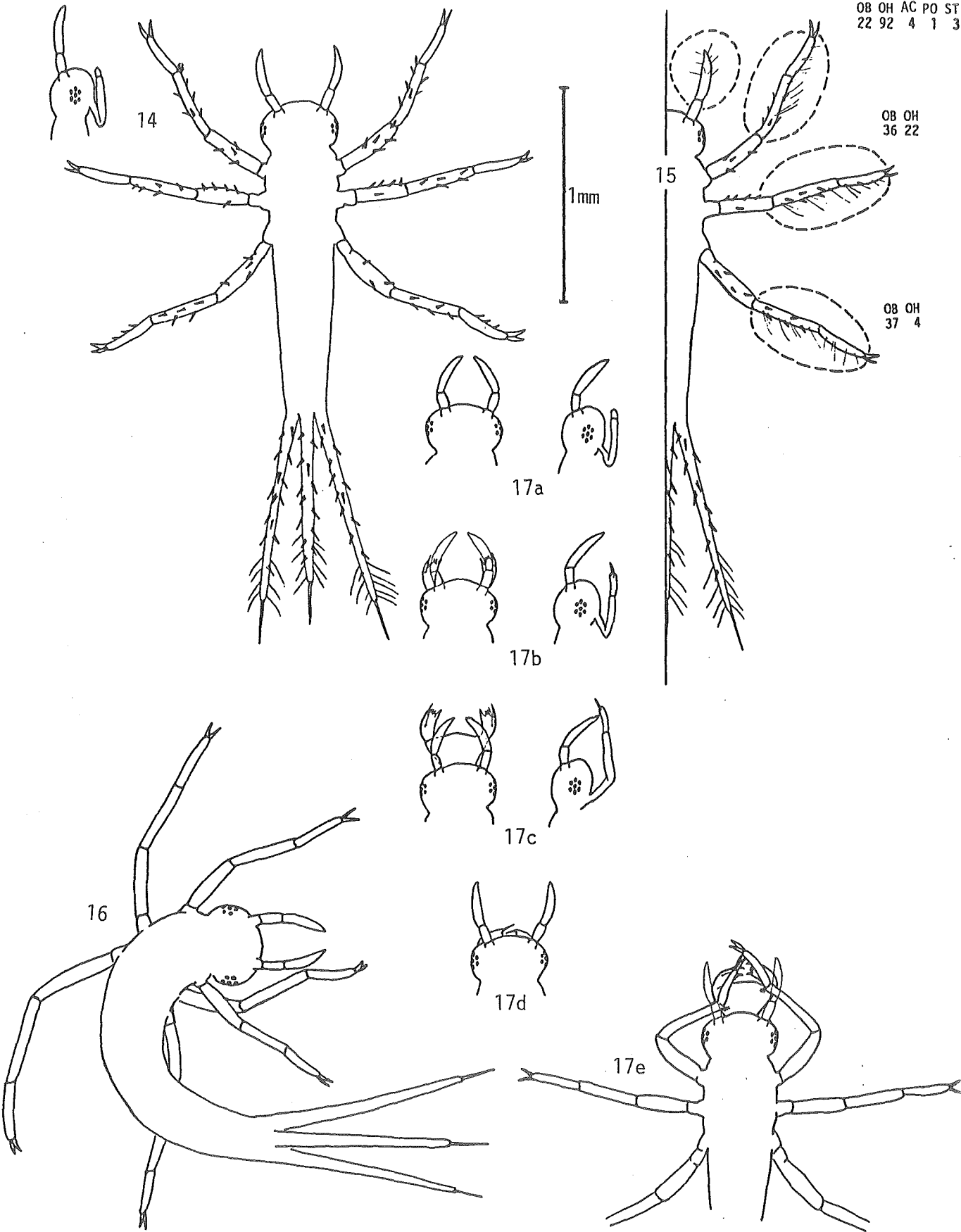
- a) antennae close
- b) palp open
- c) strike
- d) chew
- e) clean.

OB OH AC PO ST
1 5 13 2 14

OB OH AC PO ST
22 92 4 1 3

OB OH
36 22

OB OH
37 4



substrate with their other legs. The hind legs were then returned to the leg spread position. This behaviour appeared to be associated with observed movements of nematodes in the detritus under the larva.

4) Orient body (OB) (Fig. 16)

The larva turned its body to point the head towards a point of prey contact. This behaviour usually involved leg movement and when prey contact was with hind or mid tibia or tarsi could be complex.

5) Orient head (OH)

The larva turned its head, without leg movement, and aimed the head towards a point of prey contact.

6) Antennae close (AC) (Fig. 17)

The antennae were drawn together along the axis of the body with apices opposing. There was a strong, stereotyped, ventral flexion at the pedicel-flagellum joint.

7) Palp open (PO) (Fig. 17b)

The larva extended its palps rapidly so that, in dorsal view, they lay below the antennae. This posture was held for 0.5–5 s. (Note: palps always open at the commencement of a labial strike).

8) Strike (ST) (Fig. 17c)

The larva projected its labium forward in the direction of prey. (this behaviour category includes palp opening if the strike was not preceded by 'palp open' defined above).

9) Grasp (GR)

The labial palps were closed back against the prementum, securing the prey animal which was then drawn back to the buccal cavity.

10) Chew (CH) (Fig. 17d)

The grasped prey was attacked and broken up by mandibles and maxillae. While chewing there were frequent small movements of labium and palps which repositioned the prey.

11) Reject (RE)

The larva opened its labial palps and extended its labium forward and released the prey. This motor pattern was sometimes repeated, at least in part, several times until the prey (or prey remains) were ejected.

12) Ingest (IN)

The broken up remains of prey were taken in through the buccal cavity and passed down the oesophagus.

13) Clean (CL) (Fig. 17e)

The labium was extended slowly and then the specialised setae of the apical comb (located near the distal end of each fore tibia) were scraped forward over the inner face of the labium. Forelegs were moved alternately. Palps and labium may be flexed repeatedly during this operation. Often larvae retracted the labium, rested for a few seconds, and then repeated the cleaning actions.

Two additional behaviours, 'stalk' and 'nod', were observed while larvae were preying on crustaceans but were not incorporated in the transition arrays for analysis.

14) 'Stalk'

This behaviour involved the orientation of the body towards a feeding crustacean followed by a slow, walking advance until contact was made. Cladocerans and copepods were detected up to one body length from a leg spread position larva and the 'stalk' was initiated. 'Stalking' ceased if another prey animal contacted the larva.

15) 'Nod'

This occurred when a larva was chewing on a cladoceran. The larva nodded its head in a dorso-ventral arc.

On occasions larvae opened and closed their labial palps several times in rapid succession. This pattern, 'mumbling', was not distinguished from 'palp open' in this analysis.

Prey detection and larval responses

Larvae responded to prey contacting their antennae, tibiae or tarsi. Prey touching the head also elicited predatory responses, but contact with the trunk of the body or the caudal lamellae was generally ignored. On a few occasions grooming motions occurred apparently in response to prey contact. In addition to spiniform setae distributed over the body, antennae, tibiae and tarsi possess a number of long fine setae on their dorsal surfaces which appear to act as mechanoreceptors. The distribution of these setae and the dimensions of the tactile sensory space are indicated in Fig. 15.

Larval responses to harpacticoid prey differed depending on which of the sensory areas had been contacted (Fig. 15). Sensitivity to non-tactile stimulation (perhaps vibrations) from distant prey appeared independent of the direction of the stimulus (Fig. 18); similar detection ranges to those with P. volcanicus were also found with A. guttata prey. A. guttata settled on their backs and 'kicking' food into their mouths, were particularly attractive prey to X. zealandica larvae and almost invariably were stalked. The maximum detection range observed was about 1mm which closely approximates one body length of the second instar X. zealandica.

Behaviour patterns with different prey

The responses of larvae to various prey are summarized in Tables 5-11. These tables are transition arrays with the succeeding behaviour in the columns.

Larvae kept without prey were largely inactive and displayed no predatory responses (Table 5). The five larvae observed all failed to move more than three body lengths in the 30 min observation period.

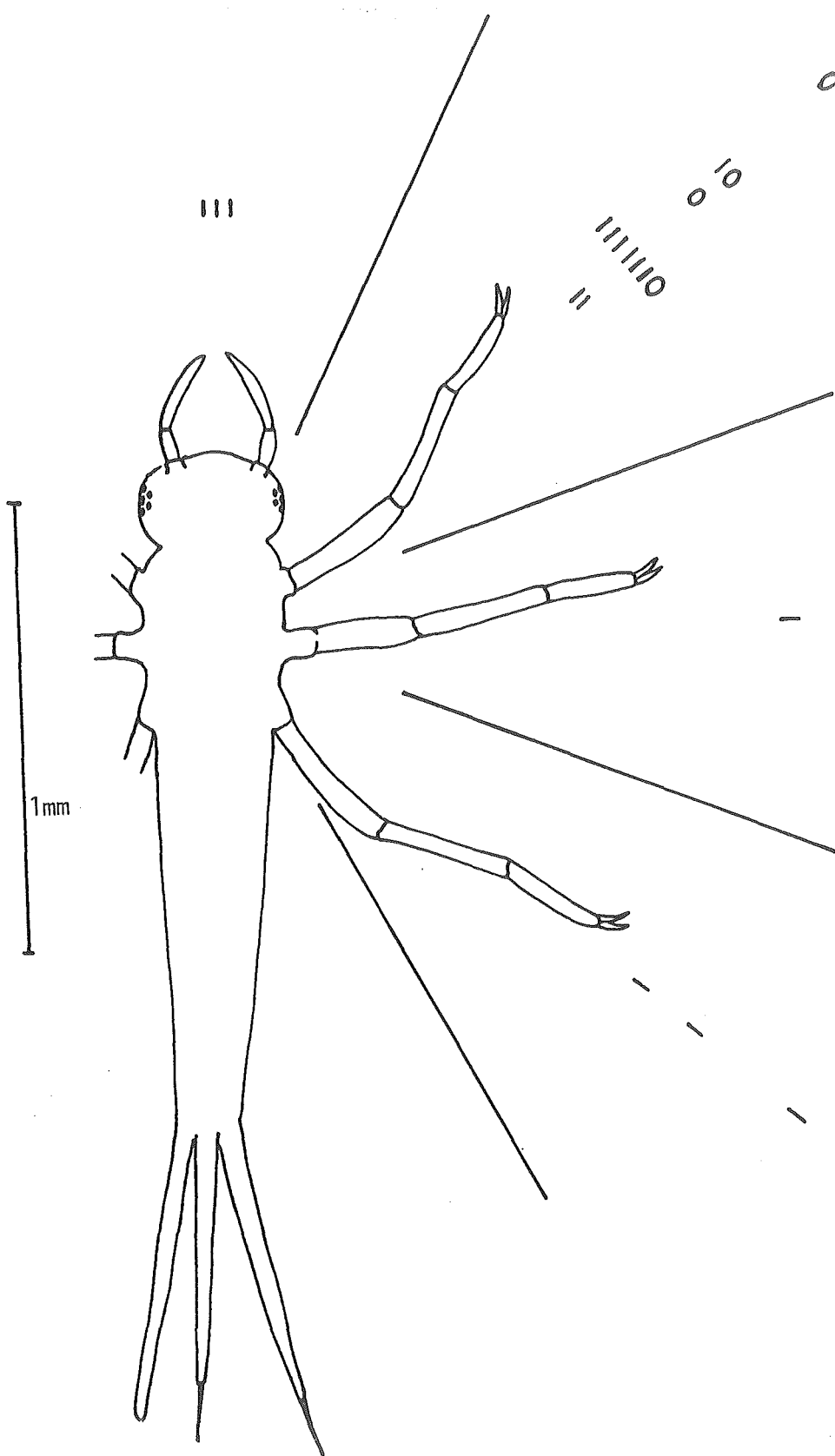


Fig. 18. Detection of prey through vibrations? The points mark the minimum separation of larva and harpacticoid prey at the commencement of stalking behaviour. Points whose sector positions were unclear in the transcript are denoted by hollow points.

Key for Tables 5 – 11.

LO	locomotion
LS	leg spread
LD	leg drag
OB	orientate body
OH	orientate head
AC	antennae close
PO	palp open
ST	strike
GR	grasp
CH	chew
RE	reject
IN	injest
CL	clean

These behaviours are described in the text.

Table 5. Transition matrix of second-instar X. zealandica larval predatory behaviours in the absence of prey.

Columns contain successor behaviours. Five larvae were each watched for 30 min. in this time 68 movements occurred. Key to symbols opposite.

	LO	LS	LD	OB	OH	AC	PO	ST	GR	CH	RE	IN	CL
LO	3	19					1						
LS	19	4	1	7		1							
LD						1	1						
OB		7											
OH													
AC		2											
PO		1	1										
ST													
GR													
CH													
RE													
IN													
CL													

Table 6. Transition matrix of second-instar X. zealandica larval predatory behaviours with Paramecium as prey.

Columns contain successor behaviours. Five larvae were each watched for 30 min. in this time 597 movements occurred. Symbols as for Table 5.

	LO	LS	LD	OB	OH	AC	PO	ST	GR	CH	RE	IN	CL
LO		2											
LS		40		41	40	11		6					2
LD		1											
OB		11			3	28	1	8					
OH		5				31	2	14					
AC		33		6	6	4	13	32					
PO		4		1	1	8		2					
ST		6				5		8	43		10		3
GR										28	15		
CH											28		
RE	1	5		3	1	2		4					37
IN													
CL		33	1		1	5		1					1

Table 7. Transition matrix of second-instar X. zealandica larval
predatory behaviours with rotifers as prey.

Columns contain successor behaviours. Five larvae were each watched for 30 min. in this time 36 movements occurred. Symbols as for Table 5.

	LO	LS	LD	OB	OH	AC	PO	ST	GR	CH	RE	IN	CL
LO	5	9											1
LS	5	3		3		2							
LD													
OB						3							1
OH													
AC	2	2		1									
PO													
ST													
GR													
CH													
RE													
IN													
CL	2												

Table 8. Transition matrix of second-instar X. zealandica larval
predatory behaviours with nematodes at low density as prey.

Columns contain successor behaviours. In 2½h 584 movements occurred. Symbols as for Table 5.

	LO	LS	LD	OB	OH	AC	PO	ST	GR	CH	RE	IN	CL
LO	50	38			1	2							9
LS	25	12		30	13	10							8
LD	2	1				1							1
OB		8		7	3	58	4	5					3
OH	2	3	2	5	6	36		4					
AC	4	17	1	42	32	10	10	10					3
PO		3		1	2	4		5					
ST		2		3		3		1	9		1		8
GR										9			
CH												9	
RE			1										
IN	2	3											4
CL	15	11	1		1	5	1	2					

Table 9. Transition matrix of second-instar X. zealandica larval predatory behaviours with nematodes at high density as prey. Columns contain successor behaviours. In 2½h 671 movements occurred. Symbols as for Table 5.

	LO	LS	LD	OB	OH	AC	PO	ST	GR	CH	RE	IN	CL
LO	5	21	3	1	1	6	1	1					2
LS	6	11	1	45	8	18	4	7					2
LD	4	2		3		2	1						1
OB	1	17	2	6	5	32	10	18	1				1
OH	1	5		8	1	10	4	1					
AC	3	16	2	12	12	1	31	15					2
PO	1	6	2	8	3	10	3	24					
ST		7		5		4	2	25	44	1	1		2
GR			1							43	1		
CH	1			1							1	40	1
RE		1		1		1							
IN	8	13	1	3		7							8
CL	10	3	1			3	1						

Table 10. Transition matrix of second-instar X. zealandica larval predatory behaviours with Alona as prey. Columns contain successor behaviours. In 2½h 1022 movements occurred. Symbols as for Table 5.

	LO	LS	LD	OB	OH	AC	PO	ST	GR	CH	RE	IN	CL
LO	3	38		1		1				1			4
LS	13	53	1	143	12	32	6	6		1		1	4
LD	2	1	1	1		1							
OB	6	56	1	12	7	92	12	27		1			1
OH		1		6	4	8	1	6					1
AC	5	51	2	29	7	7	28	42					3
PO		10	1	10	2	11	1	15					1
ST	6	32		9		9	3	17	32		2		13
GR	1	2		1		5	1	7		14			2
CH	1	1		2		1		2				4	7
RE		1											1
IN	1	3											1
CL	8	23		3		2		2		1			3

Fig. 19. Flow diagram of larval behaviour sequences with Paramecium prey. This information is abstracted from Table 6. Orientate head and orientate body appear to be one category when larvae are attacking Paramecium.

Solid lines indicate transitions occurring with $\geq 50\%$ probability.

Dashed lines indicate transitions occurring with probabilities between 20% and 50%.

Dotted lines indicate transitions occurring with probabilities between 10% and 20%.

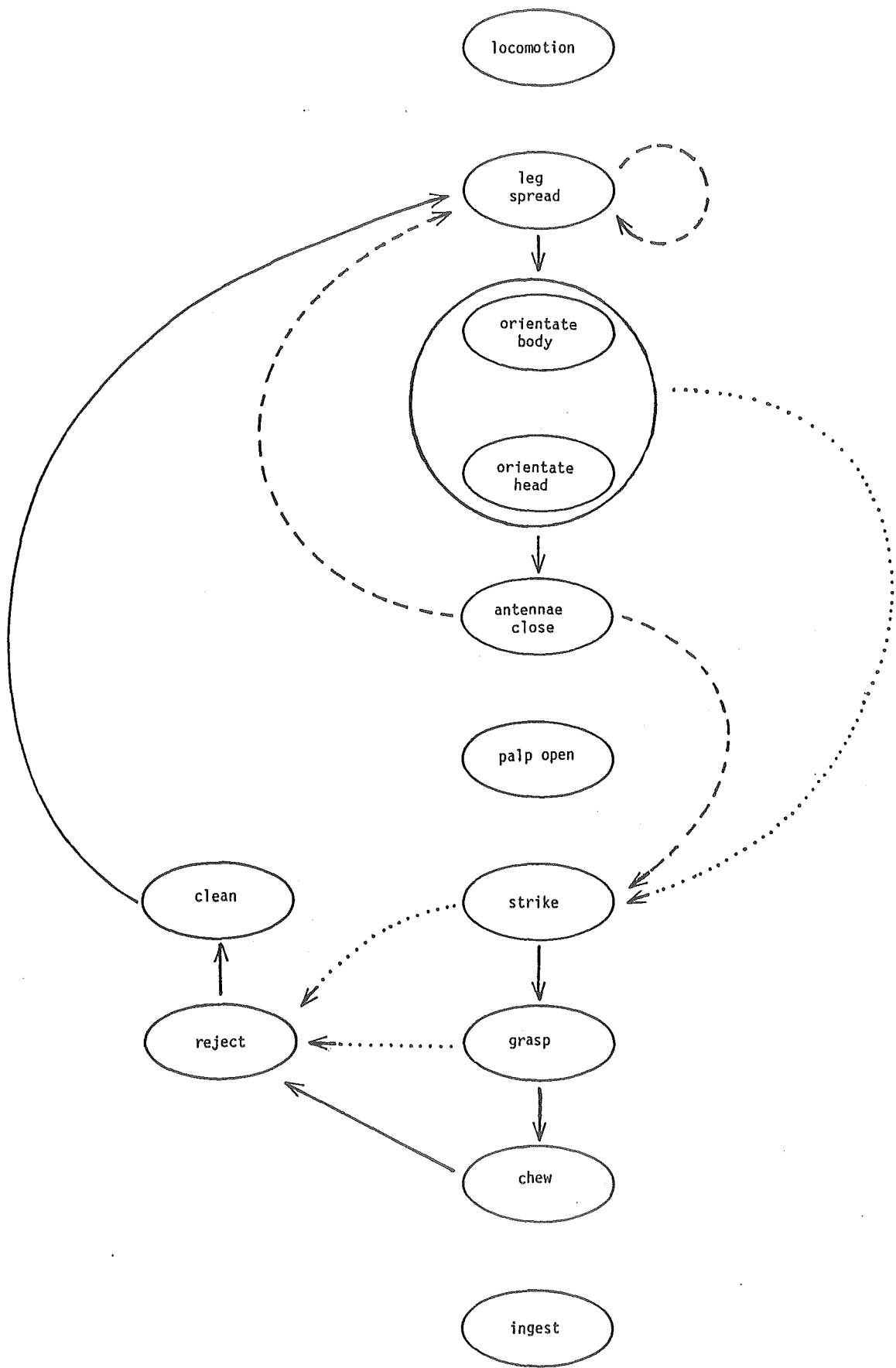


Fig. 20. Flow diagram of larval behaviour sequences with nematodes as prey. This information is abstracted from Table 8.

Solid lines indicate transitions occurring with $\geq 50\%$ probability.

Dashed lines indicate transitions occurring with probabilities between 20% and 50%.

Dotted lines indicate transitions occurring with probabilities between 10% and 20%.

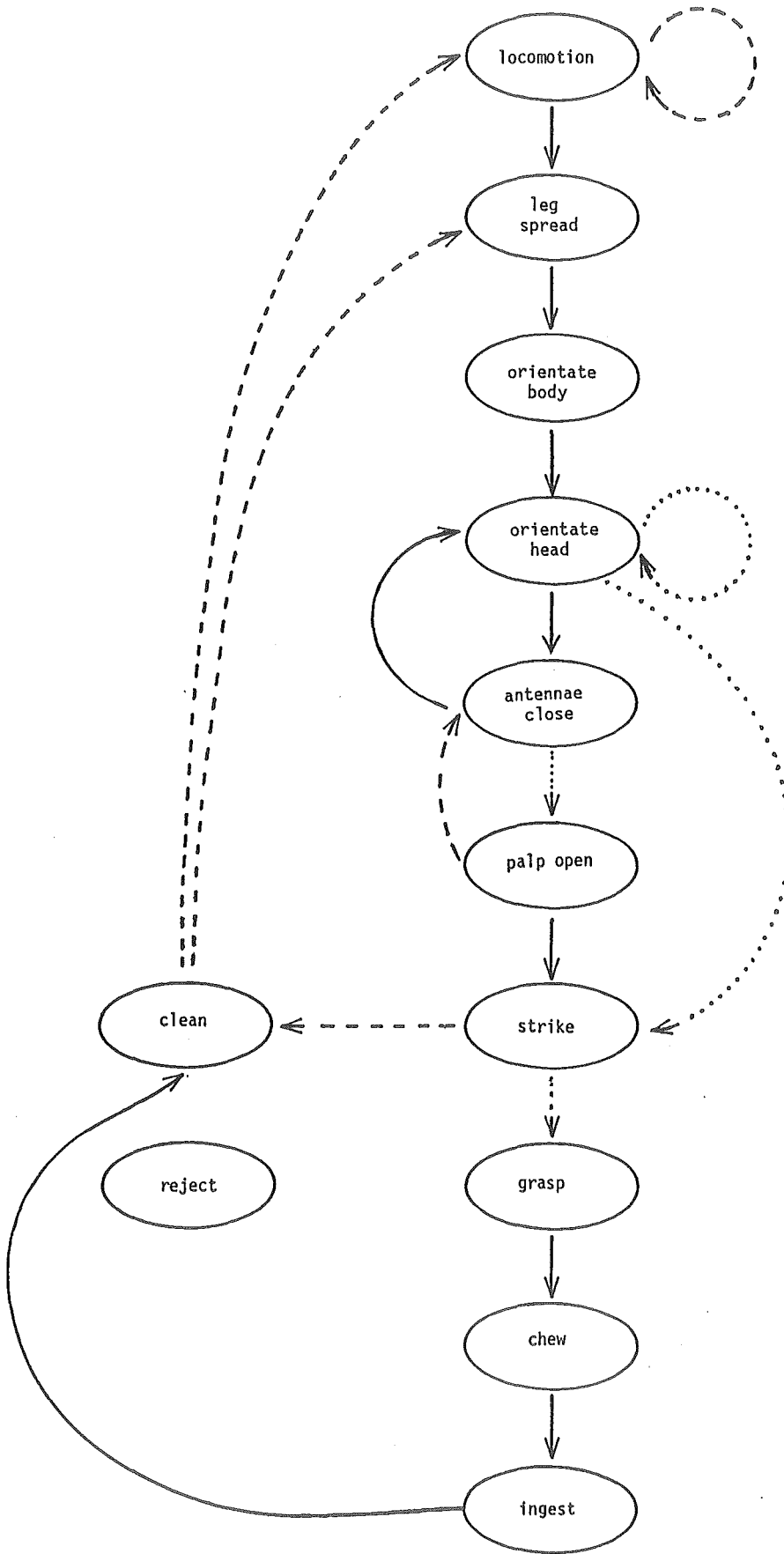


Fig. 21. Flow diagram of larval behaviour sequences with harpactacoids as prey. This information is abstracted from Table 11. Note how complex the behaviour is in contrast to Figs 19 and 20. Solid lines indicate transitions occurring with $\geq 50\%$ probability. Dashed lines indicate transitions occurring with probabilities between 20% and 50%. Dotted lines indicate transitions occurring with probabilities between 10% and 20%.

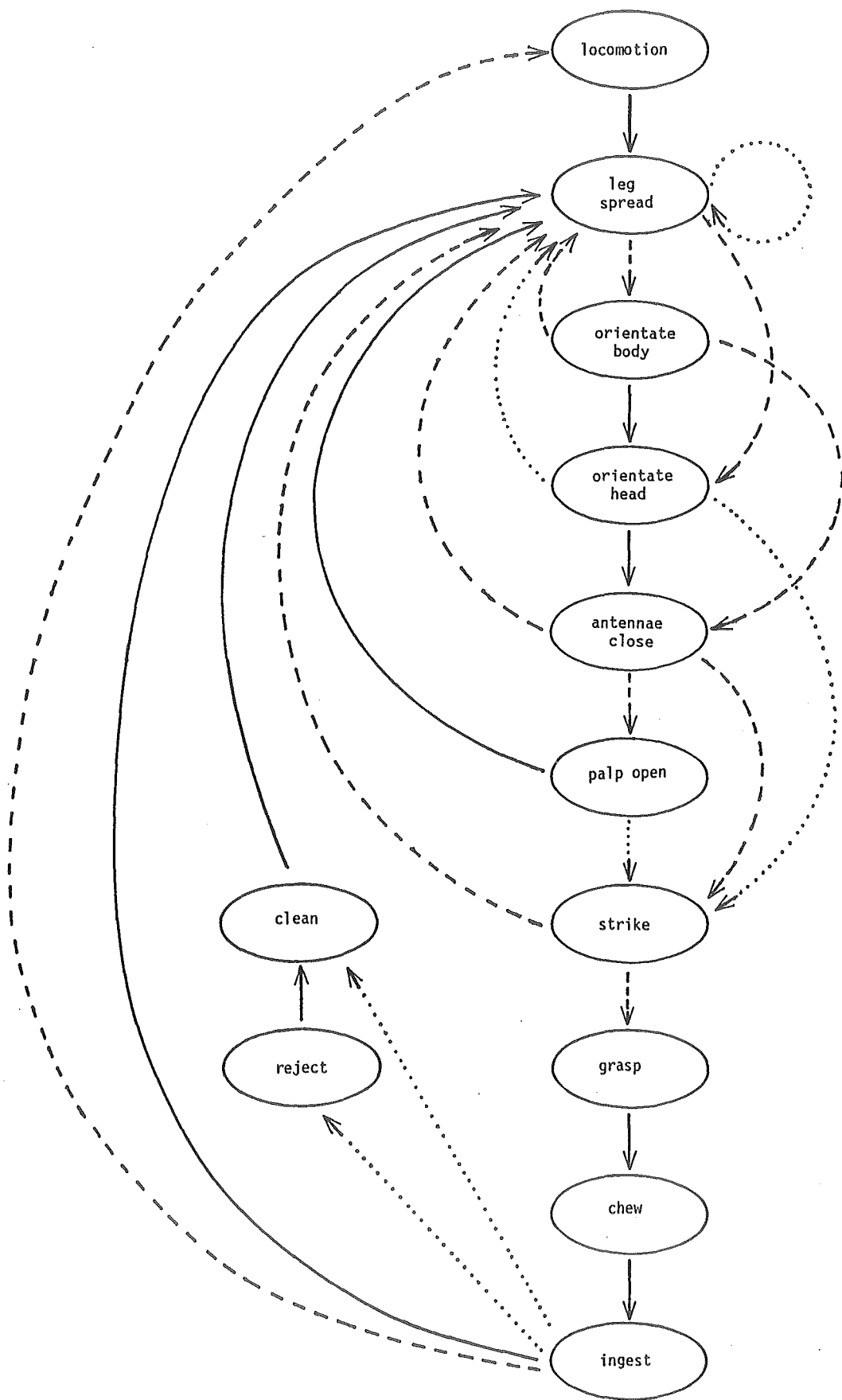


Table 11. Transition matrix of second-instar X. zealandica larval predatory behaviours with Phyllognathopus as prey.

Columns contain successor behaviours. In 2½h 563 movements occurred. Symbols as for Table 5.

	LO	LS	LD	OB	OH	AC	PO	ST	GR	CH	RE	IN	CL
LO		12											2
LS	6	18		63	53	10	2	4	1				4
LD		1											
OB	1	18		2	31	15		1					1
OH		10		1		63	5	9					1
AC	3	36	1	2	4	3	20	28					1
PO		24		1		2		3					
ST	1	19			1	4	3	5	11				7
GR										9		2	1
CH						1	1					7	
RE													1
IN	2	5									1		1
CL		19											

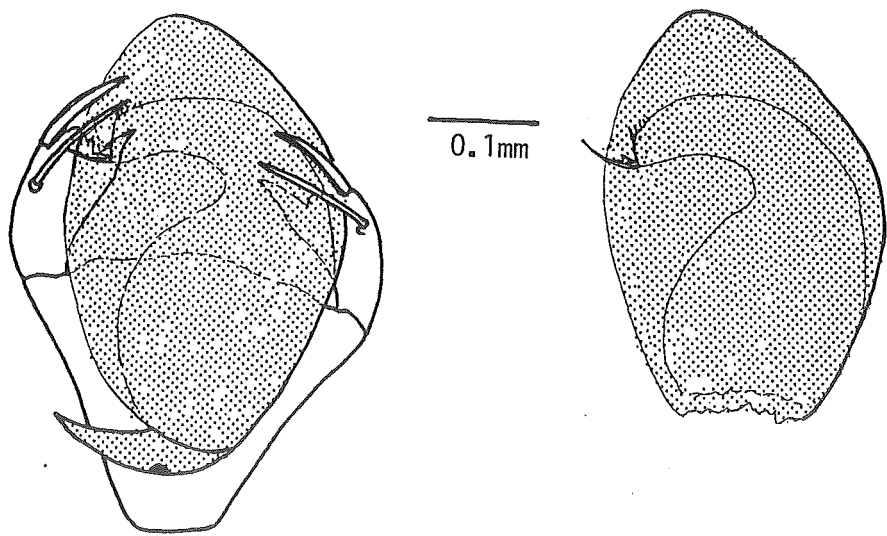


Fig. 22. Predation on Alona. This type of prey was captured only when it lay head first in the plane of the labium with its body held against the end hook by the movable hook and seta (left). Even when held in this position only the head and a small quantity of the thorax were consumed (right). The mandibles of the X. zealandica larva appeared unable to penetrate the valves.

Paramecium moved quickly and smoothly within the water column and immediately above the floor of the watchglass. Larvae responded rapidly to contact with Paramecium by orienting their bodies or heads and initiating an antennae close. Paramecium which made contact with the antennae during antennae close were struck at immediately. No period of preliminary palp opening or pause was observed before a strike (Table 6). The first few Paramecium captured by a larva were grasped, drawn to the buccal cavity and chewed. The larva then stopped chewing, paused for a few seconds and ejected the prey. Ejection movements were often repeated several times in quick succession, even after the Paramecium had moved away. Immediately after rejecting a prey item, the larva cleaned its labium and palps intensively for 10-30s before resuming the leg spread position. As a feeding bout progressed, larvae responded less frequently to prey contact and required less and less time to reject prey. Finally, larvae were striking and rejecting prey without grasping them (Table 6). This rejection was not simply the result of inept predatory activity but involved a failure to close the palps on an otherwise captured prey item (Paramecium appeared very easy to capture, and naive animals had almost 100% success in grasping them and chewing them). A Paramecium which had been chewed sometimes suffered major damage and sank to the bottom where it had been dropped. However, for the most part these ciliates were able to swim away, albeit sometimes in an uncoordinated fashion. Unchewed Paramecium swam off with no sign of injury.

Rotifers elicited no predatory responses from X. zealandica larvae (Table 7).

Nematodes were usually burrowing through detritus on the floor of the watchglass when they excited X. zealandica larvae. In experiments with nematodes, dragonfly larvae spent much of their time circling and adjusting position apparently in response to nematode activity in the substrate beneath their feet (Tables 8, 9). Nematodes were protected by

the surrounding detritus and striking larvae frequently collected a labium full of plant material which was cleaned off before searching behaviour recommenced.

Larvae responded rapidly to contact with A. guttata but appeared to have great difficulty capturing this species (Table 10). Prey was successfully localised and attacked but few larvae were able to grasp Alona successfully as the large curved faces of the cladoceran valves appeared to slide out of the grasp of the labial palps. The few large Alona eaten were all captured so they lay on the labium with their heads directed at the buccal cavity (Fig. 22). This prey orientation appeared to be attained fortuitously and resulted in the larva being able to eat the cladoceran's head (Fig. 22). This took 6-8 min of chewing, a handling time much greater than that observed with other prey. Larvae appeared to be unable to retract the labium fully after capturing A. guttata and often nodded their heads up and down while chewing. Smaller Alona were taken successfully, but many managed to work their way out of the labium while the dragonfly's mandibles were working on the valves. Alona captured by the postabdomen usually jerked free.

Harpactacoid nauplii seemed vulnerable to attack from any direction and were readily preyed upon (Table 11). Handling time with this prey was only a few seconds: nauplii were drawn to the mandibles, masticated a few times and then swallowed. Subadult and adult P. volcanicus were vulnerable when caught head on and, although the handling time was of the order of 1-2 min, they were consumed. Animals not caught head on, but still grasped and drawn back to the buccal cavity often were able to escape. The gape of the larval dragonfly was too small to permit the mandibles to pierce the carapace; the sclerites of the harpactacoid's body appeared to be highly flexible and few incisions were achieved while chewing the body. The major articulation of the thorax, however, was vulnerable to attack. During the prolonged periods that X.

zealandica spent chewing at sclerites, many harpactacoids were able to work their way out of the labium and effect an escape. Subadults and adults caught by the abdomen or tail almost invariably were able to free themselves by thrashing about. During the observations two adult and two subadult harpactacoids were captured head on and consumed; six further subadults and six nauplii were also eaten. Whereas three adults were grasped, but escaped when the X. zealandica larva was unable to penetrate the carapace; five further adults and subadults captured by the tails corkscrewed free and two nauplii which perched on the heads of X. zealandica larvae escaped also.

The food bolus from an adult P. volcanicus filled the dragonfly larva's gut from the buccal cavity to the base of the hind legs. X. zealandica larvae ceased to display any interest in prey after consuming such an item. On one occasion an adult P. volcanicus abdomen broke off and fell to the floor while the predator was eating the thorax. Seven seconds after the thorax had been consumed the larva moved forward, retrieved and ate the abdomen. On another occasion a X. zealandica larva was seen to attack and capture a subadult P. volcanicus while the remains of the previous prey item were still held in the labium.

Differences in sequences

In addition to the presence of such apparently prey specific behaviours as 'leg drag', which was almost entirely restricted to larvae feeding on nematodes, and rejection of prey, which was associated with Paramecium, differences in behaviour sequences occurred with different prey. The successor behaviours to 'leg spread', 'strike' and chew were compared for each of the prey types (Table 12).

Table 12. Comparison of key rows of the transition matrices of predatory behaviour sequences produced when X. zealandica second-instar larvae fed on Paramecium, nematodes, Alona and harpactacoid prey.

Rows LS, ST and CH were extracted from Tables 6, 8, 9, 10 and 11 and frequencies of succeeding behaviours were examined for each prey pair using chi-square tests. Because of the need to suppress cells with low expectation values X^2 values are not directly comparable. Behaviour codes as for Tables 5 – 11. When sufficient df existed the analysis was repeated after removing the most significant cell.

row	prey species compared	approx X^2	most significant cell
LS	<u>Paramecium</u> – Nematodes	30 with 4 df 17 with 3 df	OH LS
LS	<u>Paramecium</u> – <u>Alona</u>	65 with 5 df 21 with 4 df	OH LS, OB
LS	<u>Paramecium</u> – harpactacoid	16 with 4 df 3 with 3 df	LS ns
LS	Nematodes – <u>Alona</u>	13 with 6 df 9 with 5 df	ST ns
LS	Nematodes – harpactacoid	39 with 5 df 13 with 4 df	OH LO
LS	<u>Alona</u> – harpactacoid	67 with 5 df 2 with 4 df	OH ns
ST	<u>Paramecium</u> – Nematodes	10 with 4 df	ns
ST	<u>Paramecium</u> – <u>Alona</u>	26 with 4 df	GR, CH
ST	<u>Paramecium</u> – harpactacoid	22 with 3 df	LS, GR
ST	Nematodes – <u>Alona</u>	27 with 4 df 3 with 3 df	LS ns
ST	Nematodes – harpactacoid	28 with 3 df 3 with 2 df	LS ns
ST	<u>Alona</u> – harpactacoid	2 with 3 df	ns
CH	<u>Paramecium</u> – all others	large, 1 df	RE
CH	Nematodes – <u>Alona</u>	26 with 1 df	CL

Response to unpalatable prey

The behaviour of X. zealandica feeding on Paramecium was consistent with learning having occurred. During the course of each experiment, larvae displayed a diminishing interest in predatory activity and towards the end of the experimental period often received many prey contacts before responding. The method of data collection precluded any analysis of this temporal phenomenon. The sequences of responses were, however, available for analysis (Table 13). The order of occurrence of

Table 13. Sequences of responses of X. zealandica second instar larvae attacking Paramecium

F represents a full attack sequence viz strike, grasp, chew and reject; P denotes an attack without the chew behaviour and P' denotes an attack lacking both grasp and chew components. Attacks which were not followed by a bout of cleaning are asterisked. The distribution of full and partial (F and P) attacks within each sequence are compared using the Mann-Whitney U test. U values and the associated probabilities of random interspersions of F and P attacks within each sequence are presented in the right hand columns. Partial attacks occur later in the sequences.

larva N ^o	sequence of attacks	U	P<
9	F, F, F, F, P, P, F, F, F, P	15	.2
10	F, F*, F, F, P, F, P, P, P, P*, P, F, F, F, F, F	31	.5
11	F*, F, F, F*, P, P'*, F, F, F, P', P, P', F	29	.2
12	F, F, F, P, P, P', P', P', P', P, P, P', P', P'	33	.01

The total numbers of attacks (10, 16, 13, 14) are compatible with a Poisson (random) distribution which is to be expected as larvae were responding to the random arrival of prey. The numbers of partial sequences is not so well behaved.

full and partial behavioural sequences was examined for each larva (here designated by its series position number) using the Mann-Whitney U-test. Of the individuals examined, larva 10 showed no discernible difference in location within the sequence of the two forms of behaviour whereas larvae 9 and 11 displayed a weak tendency for partial responses to occur later in the series. Larva 12 produced a highly significant separation of the two behaviours indicative of associative learning having occurred. Omitting larva 12 from further analysis and examining the remaining larvae as a group we find that while overall 14 of 39 acts were partial sequences it is not until the fifth act in each individual series that a partial sequence appears. If partial sequences were distributed at random the probability of such a preponderance of full sequences occurring at the head of the series is less than 1%. When the last four acts observed in each series are examined, 4 of 12 were partial sequences (probability 0.5). Changes of response, and partial sequences, were not observed when larvae were feeding on palatable prey.

Predatory activity of older larvae

The predatory activities of later instar larvae were hard to observe for a variety of reasons (introduction to section 3). Predatory behaviour tended to be sudden and often occurred without any observed 'intention' movement. Observations on tenth instar larvae feeding on A. guttata and P. volcanicus showed marked changes in comparison to second instar larvae. Tenth instar larvae did not react to prey touching their middle and hind pairs of legs, but remained motionless. When prey touched the fore femur, the larva oriented its head and then 'plucked off' the prey with a slow, partial extension of the labium, an action of muscular rather than hydrodynamic origin. Prey detection appeared to be visual, prey passing through mid water in front of a larva's head were more readily attacked than animals on the substrate. No antennal movement

preceded a predatory strike. Smaller prey items like harpacticoid nauplii were ignored completely even by hungry larvae.

Older larvae of X. zealandica are able to scavenge in addition to using the usual active predation, characteristic of the Odonata. This tactic enables them to utilise larger items opportunistically and may account for the presence in the diet both of species they appear unable to prey on in the laboratory and for records of cannibalism in this territorial species with ritualised threat displays. This will be considered in more detail in the following chapter.

DISCUSSION

Prey detection in second instar X. zealandica larvae is for the most part tactile although non-tactile detection at a distance, probably through displacement waves or vibrations, occurred with crustacean prey. Larvae were observed to respond to prey up to one body length away, although the detection range is almost certainly greater this. Vision appears to be extremely limited in this instar, each compound eye having only seven ommatidia, and effective resolution of shape is improbable. The visual senses develop rapidly in X. zealandica (Chapter 2) and later instar larvae appear to rely heavily on vision although they also use non-visual senses in detecting conspecifics (Chapter 2) and prey (Chapter 5, 6).

The predatory behaviour of small insect larvae may be more complex than has traditionally been considered the case. Thus, Stubbs (1980) found that fourth instar larvae of the coleopteran Coccinella septempunctata (L.), previously considered to be foragers dependent on physical contact to detect prey, were able find prey using a chemical sense at a range of 0.8 cm. The performance of this larval beetle closely resembles that of second instar X. zealandica. The larval coccinellid

possesses only six ommatidia and so is unlikely to be more competent visually than second instar X. zealandica, yet it too can detect and orient to prey at a range of about one body length.

The initial responses of second instar X. zealandica larvae to contact with harpactacoid prey are summarised in Fig. 15. Responses varied in an adaptive fashion to contacts with different sensory areas. In all cases of contact with middle or hind tibiae or tarsi, and often when the forelimbs were the contact point, larvae had to orient their bodies to attack the prey items. In all but one of some 200 occasions, larvae were observed to pivot on the contacted leg, showing coordination patterns similar to those illustrated for final instar larvae of Cordulia shurtleffi Scudder larvae (Odonata: Corduliidae) by Pritchard (1965). On one occasion a larva raised its leg and did not turn. Orientation of the body was well coordinated, the turn consisting of a single smooth movement. Similar coordination was shown with all prey species and in all but a very few cases of the more than 1000 turns observed the larva completed the movement with its head and antennae pointing at the spot where the prey contact had occurred. Orientation of the body was followed most frequently by antennal search movements in the vicinity of the contact point. That the behaviours were independent was shown with harpactacoid prey, when orienting the body was followed most frequently by head orienting behaviour; this reflected the rapid jerky movements of the harpactacoids, very few of which were still near the point of contact by the time the larva had completed its turning movement.

Although statistically significant changes in the frequency of occurrence of behavioural sequences have been demonstrated in larvae fed unpalatable prey, such changes did not occur with palatable prey. The failure of one larva to produce the expected adaptive responses during the course of an experiment might be explained by the variability

found typically in learning rates.

It is not surprising that an opportunistic, polyphagous predator inhabiting a complex and sensorially chaotic environment should have flexible prey acquisition behaviours. There is evidence for both learned and unlearned prey recognition in larval Odonata (Appendix 2). However, what is surprising, is that learning apparently occurs so early in the life of X. zealandica. The central nervous system of a second instar X. zealandica weighs about 1 μ g, yet is capable of producing a high degree of spatial coordination when attacking prey and when detecting or orienting to prey at a distance. The limited sensory capacity of these small larvae would be expected to make discrimination of unpalatable prey difficult, thus the apparent inability to discriminate before making a predatory attack is not surprising. Learning has been demonstrated previously in a number of insects in situations comparable to those described here. Some orthopterans, mantids, carabids, coccinellids and formicids learn to reject noxious prey in the laboratory (Berenbaum & Miliczky 1984) and Pheidole dentata (Hymenoptera: Formicidae) have been shown to have learned enemy specification (Carlin & Johnston 1984).

Predation on Paramecium by X.zealandica was almost certainly being thwarted by the trichocyst defence mechanism of the ciliate. Although trichocysts might not be expected to pierce the chitinous exoskeleton of even a small insect larva, they could stimulate both sensillae and sensory pits in the buccal cavity region. The latency of the initial rejection response, the cleaning behaviour seen, and the lack of apparent damage to most of the attacked Paramecium are consistent with such an explanation.

Many authors (e.g. Gardiner 1951, Hutchinson 1976, Lawton 1970b) have referred to young odonate larvae preying on ciliates, specifically Paramecium, on some occasions. I attempted to feed second instar larvae of three zygopterans and six anisopterans on three species of

Paramecium and feeding attempts were always followed immediately by rejection and cleaning behaviour as described above.

Lawton (1970b) used two 'food preference cultures' with second instar P. nymphula larvae. The first comprised Paramecium, Euglena, Stylonychia, Amoeba and a rotifer species; of 52 'captures or attempted captures', 25 were on the 'abundant' Paramecium. The second culture comprised Paramecium and the cladocerans Chydorus and Daphnia obtusa; here only 4 of 62 attacks made were on the 'abundant' Paramecium. With third instar larvae, 'Paramecium was rarely taken'. Lawton speculated that this might be due to the increased ability of larger larvae to attack cladocerans instead. Such a rapid diet change on the basis of prey size would be exceptional in Odonata as noted by Thompson (1978b) who found that, in general, maximum prey size increases but smaller prey are not lost from the diet as larvae grow. I found that tenth instar larvae of X. zealandica, despite being some ten times longer than second instar larvae, still preyed on the same sized harpacticoid copepods utilised by second instar larvae; only the smallest harpacticoid nauplii were taken by second instar larvae but ignored by the tenth instar larvae. It is possible that Lawton mistook attacks on Paramecium for successful prey capture.

Prey rejection by young odonate larvae has been recorded previously by Gardner (1951) and Lawton (1970b). Gardner found that young Sympetrum striolatum (Charpentier) Anisoptera: Libellulidae) rejected red water mites, and Lawton saw a second instar Pyrrhosoma nymphula reject the only Amoeba attacked during the course of his experiment.

Predatory versatility

Predatory versatility, the use of disparate, prey-specific predatory behaviours, in euryphagous predators is well documented among vertebrates but has seldom been recorded in arthropods (Curio 1976). To

display predatory versatility animals must be capable of 'recognising' different prey types; have a varied predatory repertoire and have a CNS capable of selecting an appropriate attack behaviour. The results presented in Table 12 indicate that the behaviours of second-instar X. zealandica larvae differed at a statistically significant level when they were attacking and feeding on different prey species. However, whether these differences constituted predatory versatility, or were a consequence of prey behaviour and morphology, could not be determined directly from the transition arrays.

The prey detection phase of the predatory behaviour was examined by comparing the behaviours which followed 'leg spread'. As was to be expected, there was no significant difference in behaviour pattern between the two densities of nematode prey. However, all other comparisons differed at a high level of significance. In the cases where statistical significance is due to large contributions to the Chi-square value from the 'leg spread' cell then aspects of prey behaviour and density are responsible and this is not evidence of predatory versatility.

When the responses to Paramecium and Alona are compared (Table 12) it is apparent that they differed mainly in the orientation behaviours. With Paramecium, larvae tended to orientate their head, while with Alona orientation of the whole body was common. This was a consequence of larvae responding to Paramecium only near the front of their bodies while responses to Alona occurred over a much wider arc. Phyllognathopus volcanicus which, like Paramecium, tended to be attacked when near the front of the body (Fig. 15), differed from Paramecium largely in the 'leg spread' cell and from Alona in the orientation component.

Differences in the orientation components showed that the dragonfly larvae discriminated between different prey and hence displayed predatory

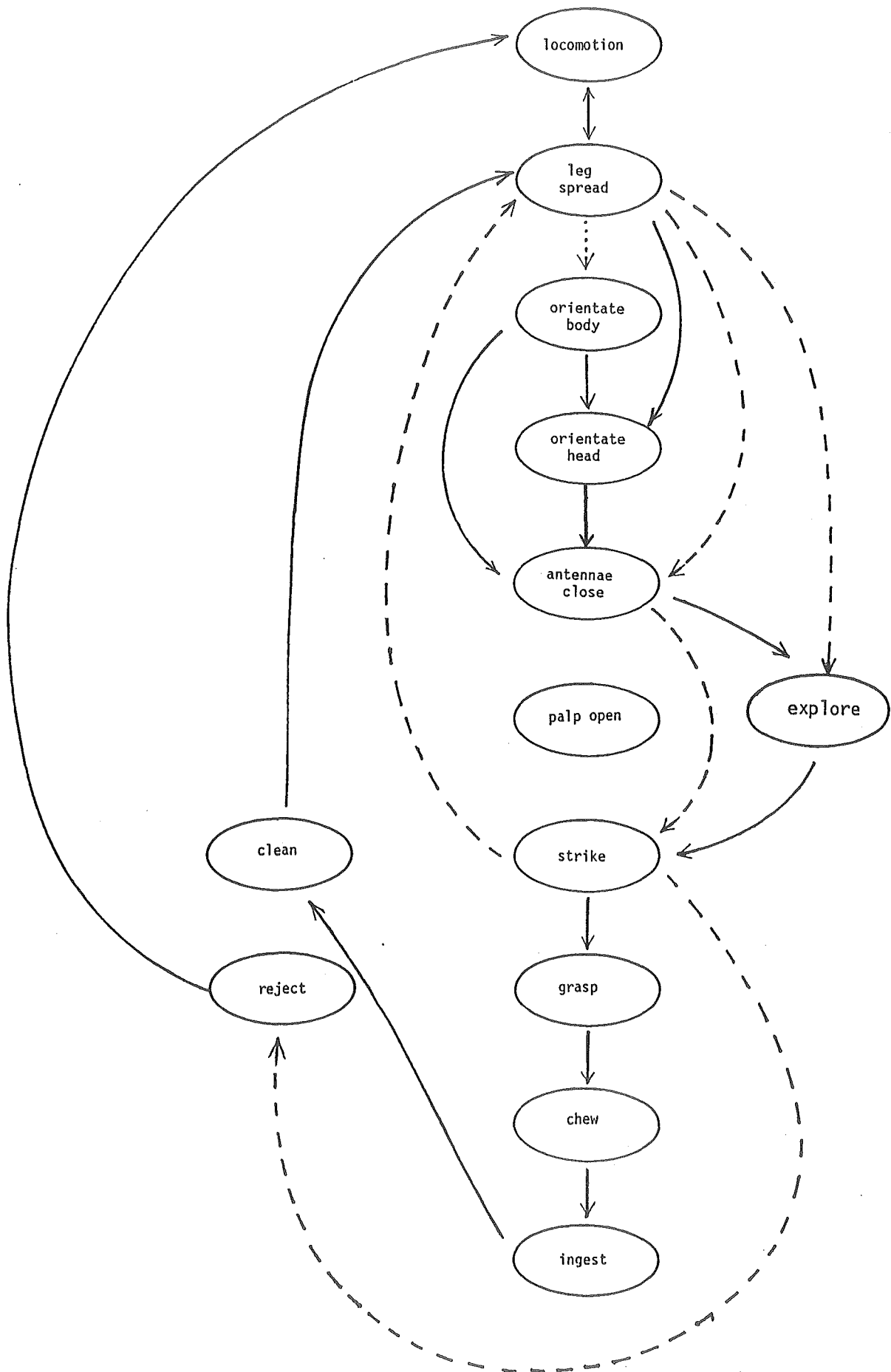
versatility.

The attack phase of the predatory behaviour pattern was examined by comparing the behaviours which followed the predatory strike. As shown (Tables 8, 9), there was no significant difference between the two nematode densities and also no difference between the two crustacean prey. Paramecium were the only prey to be rejected without grasping. This immediate rejection of Paramecium, at an unusual point in the predatory sequence, represents a form of prey discrimination and thus predatory versatility.

The consumption of prey was examined by comparing the behaviours which followed chewing. The responses with Paramecium and Alona differed from those with other prey at this stage. These differences were, however, consequences of prey morphology and do not represent predatory versatility.

Caillere (1965, 1973, 1974) produced accounts of the predatory behaviour of Calopteryx splendens. The flowchart he produced to summarise the sequences of predatory behaviours he observed is reproduced here as Fig. 23. Caillere (1974) stated that in C. splendens second instar larvae (first instar in his terminology) displayed all the predatory sequences observed in older larvae. The predatory sequences of older larvae were characterised by the suppression of intermediate components of the predatory sequence. The behaviours observed in C. splendens and those found in second instar X. zealandica differ in a number of non-trivial ways. Unlike second instar, and like older C. splendens larvae, second instar X. zealandica pivoted on a touched leg to attack prey. X. zealandica did not display the extensive prey exploration behaviours found in Calopteryx; prey exploration appears obligatory in young Calopteryx. The volume within which second instar X. zealandica larvae respond to prey contact (Fig. 15) resembles closely that of fifth instar C. splendens (Caillere 1974).

Fig. 23. Flow diagram of Calopteryx predatory behaviour (interpreted from Fig. 5 of Caillere 1965 and redrawn using the terminology of Figs 19-21). Dashed lines indicate alternative predatory sequences which occurred in older larvae.



At the eighth instar the Calopteryx antennae develop their full complement of segments, exploratory behaviours are much reduced and the larva pivots in response to stimulation of any tarsus; the 'simplification' of behaviour patterns in this instar represents what Caillere (1973) regarded as a critical stage in the development of Calopteryx predatory behaviour. The behaviour of second instar X. zealandica resembles closely that of eighth instar C. splendens larvae. In all, second instar X. zealandica appear more 'advanced' ontogenetically than the calopterygids.

Late instar X. zealandica are visual predators in daylight and omit most intermediate steps in the predatory sequence. Prey is detected, there may be a few orientation movements of the head or body, and then the larva strikes with its labium. Late instar X. zealandica are also able to catch prey in the dark, when presumably behaviours similar to those used in the younger instars are utilised. Corbet (1962) has pointed out with reference to Aeshnidae that larvae which are normally visual predators may revert to more neotonic predatory behaviours at night or under other conditions when vision is impaired. While zygopteran larvae can (and do) hunt at night this is not evidence that they are restricted to non-visual senses for prey detection.

CHAPTER 5

Scavenging behaviour of older larvae

INTRODUCTION

'It is in the larval stage of Odonata that the greatest adaptive radiation in functional morphology has taken place. This has presumably been necessitated by interspecific competition for space and food in the relatively confined aquatic habitat.' (Corbet 1962).

While Swammerdam (c. 1675) considered that dragonfly larvae fed on mud, this view was soon corrected and it has long been recognised that Odonata larvae are obligate carnivores. Furthermore it has generally been accepted that only living, moving animals elicit predatory behaviour in dragonfly larvae (e.g. Pritchard 1965a). However, Corbet (1962) interpreted the occurrence of gastropods in the diet of some aeshnids as giving the lie to the popular assumption that larval Odonata fed only on moving prey.

In a number of studies of diet, the remains of larval Zygoptera have been discovered in faecal pellets, and this has sometimes been described as 'cannibalism'. However, Chutter (1961) made the point that, in the only example he found of predation on a larval zygopteran, the identity of the prey species was uncertain, and in general it appears that predation by larval Zygoptera on larval Zygoptera is rare (Corbet 1980).

In New Zealand, Crumpton (1979) found that larvae of Xanthocnemis zealandica preyed widely on larval Zygoptera (about 10% of animals in her samples – but most records occurred in March and April), while Stark (1981) found no evidence for such predation in extensive collections from an area of lake where X. zealandica was the only recorded larval

zygopteran. Dowdle (1981) recorded two isolated instances of predation on larval Zygoptera by this species, and I have found remains of larval Zygoptera in faecal pellets of field caught X. zealandica larvae. In all cases where the remains could be identified to species they proved to be small Austrolestes colenisonis (White) (Zygoptera: Lestidae).

Field records of so called 'cannibalism' are totally at variance with my own experience with, and observations of, this territorial larva with its highly ritualised threat behaviour (Rowe 1980, Chapter 2). Even when a larva is defending its territory, labial strikes occur infrequently, and generally at ranges too great to allow contact (often at separations of more than twice the maximum labial extension). In almost every observed instance, intraspecific labial strikes were preceded by extensive mutual bouts of conspicuous caudal swinging (SCS) (Chapter 2) rather than by the cryptic behaviour seen when approaching prey species. Larval X. zealandica have rarely been seen to make errors in the range of the strike when attacking prey and this proficiency appears to be general among larvae of the Odonata (Pritchard 1964).

Preliminary observations

During my observational studies of territorial behaviour in X. zealandica (Chapter 2) a number of animals died and were inadvertently left in the aquarium. In four cases the bodies of these animals were eaten by other larvae and a number of larvae which moulted in aquaria were found partly eaten 2-4 days after ecdysis. These occurrences suggest cannibalism but death from other causes followed by scavenging could not be ruled out.

METHODS

X. zealandica larvae were obtained by dip-netting from a pond near Cass. Larvae were introduced to standard sized (15 x 15 x 5 cm) aquaria and were allowed to settle for 2-6 days on a territorial perch

(Rowe 1980). During this period they were fed ad libitum with Lumbriculus variegatus Muller or Daphnia carinata King. Prey was removed prior to the beginning of an experiment.

To investigate the potential for cannibalism on younger instars, final instar X. zealandica larvae, in an aquarium with a single territorial perch, were presented with conspecifics several instars smaller and within prey size range. The larvae were left without other food for 1-2 weeks.

To investigate scavenging, final instar X. zealandica larvae were presented with the carcasses of a variety of insects and gastropods. Prey were killed by immersion in hot (about 50°C) water for 30s-1 min, cooled and then placed on the floors of the aquaria at various distances from the stem-perch of the resident X. zealandica larva.

Prey presented were larval A. colenisonis, Triplectides obsoleta (McLachlan) (Trichoptera: Leptoceridae) (in and out of cases), Hydrobiosidae (undet.) (Trichoptera), Periplaneta americana (L.) (Blattodea: Blattidae) of approximately the same size as the X. zealandica larvae, Physa acuta Draparnaud (Gastropoda: Pulmonata) and Potamopyrgus antipodarum (Gray) (Gastropoda: Prosobranchia). After death the bodies of the snails were drawn part way out of the shell. The size of insect prey items was such as to normally preclude predation.

A. colenisonis was used as 'bait' because live larvae of this species elicit SCS display rather than predatory behaviour from X. zealandica. A. colenisonis, T. obsoleta and the snails occurred in the habitat where X. zealandica was collected.

Hunger level

Field collections (Crumpton 1979, Dowdle 1981, Chapter 6) indicate that about 80% of larvae are likely to have food in their guts at the time of capture. Gut passage time in captivity (16°C) was about 10.25h

(S.D.=3.22 h, n = 12) (Chapter 6), indicating an equivalent 'mean time between meals' of about 13h in the field. Thus it can be assumed that larvae used in these experiments, which had been held 1-3 days without food, were under some hunger stress.

RESULTS

Cannibalism

No evidence of cannibalism was found in aquaria where young larvae were exposed to larger conspecifics. Even after a fortnight of starvation all the smaller larvae were alive, although several had lost caudal lamellae (presumably in unequal territorial encounters with the large, predatory larva). These results were consistent with those obtained in large aquaria where small and large larvae mixed in a free range situation.

Scavenging

Some individual larvae proved to be adept scavengers, but other larvae did not scavenge during the experiment.

A. colensonis as prey.

X. zealandica larvae responded to baits up to 4 cm from the bases of their territorial perches. There was a considerable variation in the time which elapsed before larvae moved to the baits. On a few occasions a larva left its stem and moved to the bait within 10 min of the bait being placed in the aquarium, on other occasions no move was made for some days, by which time the bait was black with putrefaction. Larvae appeared unable to determine the exact location of the bait before setting off, but instead tended to 'wander about' in its general direction until they made contact.

After contact was made with the carcass the larva generally moved to the head region and, after a few seconds exploration, began to chew at

the head-neck junction. Smaller carcasses were on occasion consumed where they lay; but some smaller carcasses, and all large carcasses, were moved towards the territorial perch. Small carcasses were merely dragged along, held by their head regions, as the X. zealandica larva backed towards its perch. With large A. colenisonis bodies a most unusual behaviour occurred; the X. zealandica larva grasped the carcass by the base of the wingpads then held it erect as it backed towards its perch (Fig. 24). While removing carrion to their perches X. zealandica larvae used the SCS display.

Sometimes it took larvae two or three trips to get the remains of a carcass to the base of their stem. Once on the stem the larva would back up, carrying the prey with it, before settling to feed. Any carrion left unconsumed was allowed to fall at the base of the stem and was fed on again later.

T. obsoleta as prey.

X. zealandica larvae only attacked corpses which had been removed from their cases. They appeared to have difficulty penetrating the bodies of caddis but persistent attempts were always successful. While the legs were often chewed off early in scavenging attempts, persistent attacks were concentrated on the soft abdomen rather than on the heavy sclerites of the head and thorax.

Hydrobiosidae as prey.

Dead Hydrobiosidae were consumed in a manner indistinguishable from that used for feeding on dead A. colenisonis

P. americana and snails as prey.

Carcasses of P. americana that had not been crushed tended to float and therefore were not eaten. Snails were not attacked either.

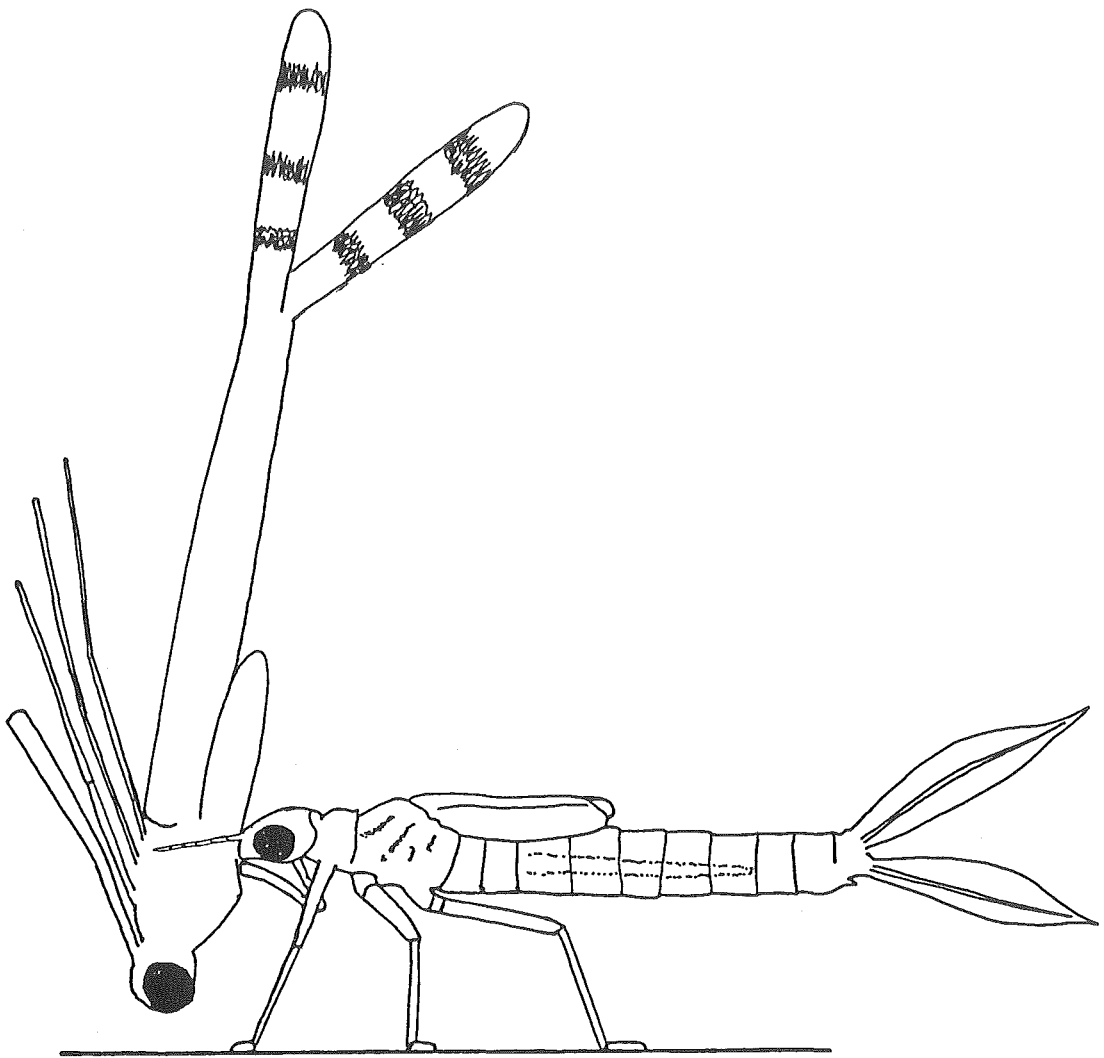


Fig. 24. *X. zealandica* larva carrying a similar sized *A. colenisonis* carcass back to the territorial perch.

Other forms of predatory versatility

X. zealandica larvae capture snails. Stark (1981) found *P. antipodarum* to be a major component of the diet of larger *X. zealandica* larvae in Lake Grasmere and during this study the remains of both *Gyraulus corinna* (Gray) (Gastropoda: Pulmonata) and *P. acuta* were found in *X. zealandica* larval faecal pellets (Chapter 6). On one occasion in the laboratory an *X. zealandica* larva was observed capturing and consuming a *G. corinna*. In contrast to *Hemianax papuensis* (Burmeister) (Anisoptera: Aeshnidae) (Appendix 2) no snail-specific predatory behaviours were observed. The larva adjusted its position by moving round the stem then, once the snail was within range, it raised its head and struck with the labium. The snail was caught by the body then lifted back to the mouthparts and consumed. As with *H.*

papuensis snail bodies were eaten out of the shell and shell fragments did not occur in faecal pellets. Similarly, there were no obvious special behaviours observed when a X. zealandica larva captured and consumed a small Hudsonema amabilis (McLachlan) (Trichoptera: Leptoceridae) by striking down to seize the head then eating the body out of the case.

Large X. zealandica larvae have highly developed vision (Chapter 2) and in the predatory behaviour observed prey detection had every appearance of being visual. However, larvae were also able to capture prey in total darkness when even such mobile prey as Daphnia carinata King (Crustacea: Cladocera) were vulnerable (Chapter 6).

DISCUSSION

Although the method of bait detection was not established, larvae were seen to leave their stem-perches soon after an A. colenisonis body was introduced. It seems reasonable to assume that chemical products escape from the carcase and diffuse, or are carried by convection, through the water, to be detected by the scavenger. The existence of a sense of taste in Odonata larvae was postulated by Pritchard (1965b), and such a sense should provide an adequate stimulus in the laboratory.

X. zealandica larvae appear to be well adapted for feeding on carrion. They will, on occasion, retrieve and consume carrion that is almost black with decay demonstrating an ability to overcome the decay byproducts produced by microorganisms (Janzen 1977). The only other odonate larvae for which consumption of carrion has been documented is H. papuensis which will feed on immobile and freshly killed snails but does not appear able to handle decaying carrion (Appendix 2).

Behaviours associated with carrion use in X. zealandica include the vertical carrying method, reminiscent of that used by leaf cutter ants, observed with long 'baits' like A. colenisonis (Fig. 24); the

removal of carcasses to the larval perch and the repeated feeding on portions of large carcasses reminiscent of caching behaviours in vertebrate predators (Curio 1976).

Corbet (1962), when considering predation on snails by aeshnid species, hypothesised that larvae which were dependent on vision for prey detection during the day might well resort to other senses and predation modalities at night. Late instar X. zealandica larvae appear to be primarily visual predators, lying in ambush for prey to pass by. The changes in behaviour exhibited when scavenging are similar to those anticipated by Corbet (1962).

The adaptive advantage of being able to utilise large dead food items that become available should be high. While the appearance of a large carcase nearby is probably not a frequent occurrence, neither is it likely to be so infrequent that adaptation towards its utilisation would be evolutionarily inconsequential. In the freshwater habitats occupied by X. zealandica larvae, adult Dytiscidae (Coleoptera), larval Chironomidae (Diptera) and larval Leptoceridae (Trichoptera) also appear to scavenge (unpubl. obs.).

While, when light levels are high, large X. zealandica larvae give every indication of being visual predators they are also able to obtain carrion using an olfactory sense and to capture prey in total darkness, presumably utilising either mechanoreceptors or detection of vibration. Given both the ability to prey on agile cladocerans in the dark and the prevalence of threat displays in response to contacts with conspecifics observed at very low (red) light levels (Chapter 2), these senses must be well developed and capable of considerable discrimination. Unfortunately, the generally cryptic behaviours and 'sit and wait', ambush tactics of X. zealandica larvae made investigation of predatory versatility in this species a difficult and inconclusive exercise.

CHAPTER 6

Feeding and site usage

INTRODUCTION

For 'sit and wait' predators which spend great lengths of time in one place and which are dependent on prey to come to them to provide food, site selection is of extreme importance. X. zealandica larvae select particular site geometries in preference to others (Chapter 8) and when on perches restrict themselves to certain micro-localities (Chapter 8). An obvious potential use of stems by larval X. zealandica is as a 'fishing site' or vantage point from which passing prey can be attacked (Macan 1964, 1977, Lawton et al 1980, Baker 1980).

On the face of it, it would appear that perch site selection in X. zealandica larvae should be explicable in terms of predatory activities. However, observed behaviour of X. zealandica larvae was not consistent with that expected if perches were selected solely as hunting sites. Larvae held in aquaria and deprived of food for significant lengths of time did not readily abandon their perches to attack prey only millimetres out of range. For example larvae which were deprived of food for 14 days and then released into a small aquarium, fought over and occupied the stems present and only those larvae unable to establish themselves on stems wandered the bottom and fed voraciously on the prey provided! In contrast, larvae which had occupied stems would not leave their perch to attack prey; instead they attempted to reach out from their perches to get within range of passing prey. These manoeuvres were usually fruitless and, as time progressed, became more exaggerated and erratic. This produced an apparent contradiction: starved predators sought, and fought over, supposed 'hunting sites' but having occupied a

site were then unwilling to take action to obtain food. In contrast, individuals which had been unable to establish a territory pursued prey and fed.

To interpret the results of laboratory studies in terms of field conditions it was necessary to have both an understanding of stem usage during attacks on prey and an estimate of feeding activity in the field. To these ends, gut passage time was established in the laboratory (using Daphnia carinata King as prey) to enable feeding rates in the field to be estimated and to find whether testing for diel periodicities in feeding in the field was feasible. Observations were made in the laboratory of larval use of perches during predatory behaviour and food consumption in the laboratory was monitored by measuring faecal pellet production. Evidence of feeding rate depression due to intraspecific interference was sought by testing for a net deficit in faecal production when two (or more) larvae shared the same site.

Diet in the field was determined by examining faecal pellets of captured larvae. Feeding rates in the field were estimated by establishing the proportion of larvae with food in the gut at capture and utilising the gut passage time established in the laboratory.

Corbet (1962: p64) suggested that 'since dragonfly larvae are facultative feeders on whatever is palatable, most readily available and of suitable size, their diet will be a reflection of their habitat'. Thus determining prey composition and prey distribution could provide an indication of the actual microhabitat occupied. The approximate size of prey taken was established in order to estimate the predation 'rate' and prey handling time.

METHODS

Penultimate and final instar larvae were collected by dipnet from Cass pond on a number of occasions and once from the littoral zone of L. Pupuke. Larvae were immediately placed in individual 75 x 25 mm vials and after 24h and 32h the vials were checked for the presence of faecal pellets.

Behaviour was observed both in large, 'free range', semipermanent aquaria where individually marked larvae (Rowe 1979) were exposed to a variety of potential prey (Lumbriculus variegatus Muller (Oligochaeta), D. carinata, Simocephalus exspinosus (Koch) (Cladocera), Opifex fuscus (Hutton) (Diptera: Culicidae)), and in small 15 x 4 x 15 cm deep cells using larvae which had been deprived of food for 2, 5 or 14 days. Some videotapes were made of behaviour in small cells.

Faecal pellets were collected from the aquarium floor using a large bore pipette. Food consumption was estimated by measuring the length of food remains contained in the peritrophic membrane of the faecal pellets (Fig. 25). The diameter of faecal pellets produced by larvae of equivalent size was quite uniform, thus length was a reasonable indicator of volume of the cylindrical faecal mass. It was easy to discriminate

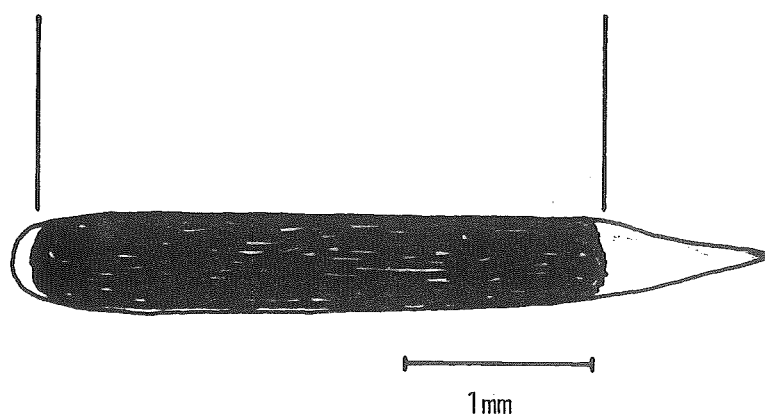


Fig. 25. Faecal pellet in peritrophic membrane, indicating the length measurement taken.

between faecal pellets (even those containing only the remains of soft prey such as lumbriculids or molluscs) and empty peritrophic membranes which were ejected at regular intervals by starving animals.

Gut passage time was determined in the laboratory for final instar larvae at 16 and 20°C under a 12h light/12h dark regime. Deacon (1979) monitored temperature through the year in a X. zealandica habitat close to my collection site and found 16°C was the highest summer temperature experienced; spot measurements at the Cass pond were consistent with Deacon's results. Prior to the experiment animals were starved for 48h to ensure they had evacuated the remains of all previous meals. Experiments were begun in the second hour of either the light or the dark phase of the cycle. Larvae were fed ad libitum for 1h on the selected food (D. carinata) and then were placed in individual 100 ml clear plastic pottles containing about 30 ml of water and a perch. Containers were examined at 1h intervals and times of faecal pellet evacuation were recorded.

RESULTS

Food consumption and gut passage time

The percentage of larvae which produced faecal pellets on any day ranged from almost 70% to 100% (Table 14).

Gut passage time varied considerably between individuals (Fig. 26). At 16°C the mean gut passage time was 10.5h (S.D. = 3.4h; n = 12) whereas at 20°C it was 9.4h (S.D. = 3.3h; n = 16). There was no difference in faecal pellet production between animals fed under room lighting and those fed in total darkness. Despite being fed for only a single one hour period, many animals produced two faecal pellets, some hours apart.

Table 14. Proportion of larvae which voided faecal pellets within 32h of capture.

collection	voided	no pellet	% with gut contents
final instar			
L. Pupuke 26 May 1980	15	1	93.75
Cass pond 24 Sept 1982	5	0	100
Cass pond 13 Mar 1983	23	7	76.7
Cass pond 20 Feb 1985	60	17	78
Cass pond 13 June 1985	21	7	75
small larvae (headwidth < 2mm)			
L. Pupuke 26 May 1980	46	20	69.7
Cass pond 20 Feb 1985	16	4	80

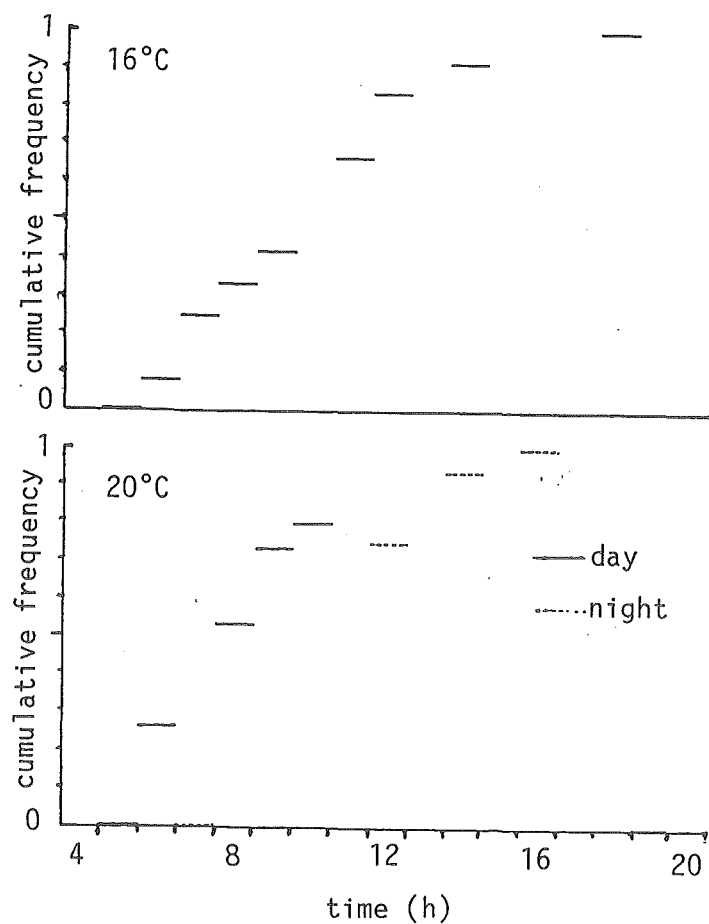


Fig. 26. Gut passage time, cumulative frequency of first faecal pellet production vs time from the end of the one hour feeding session.

Use of stem perches in predation

Under a variety of experimental conditions, X. zealandica larvae spent most of the light phase of the diel cycle at the bottom of a stem, facing downwards (Chapter 8). Prey passing by were detected visually and, if they passed within range, were often attacked. Most observed attacks involved only a larval head movement prior to the predatory strike. Infrequently, larvae would reach from the stem by releasing their fore (and sometimes middle) legs and then extending their bodies towards the prey while retaining a grip on the perch with the hind legs.

'Reaching' larvae appeared to be able to extend their attack range by 5–7 mm (Fig. 27). At night, animals moved about on their stems (Chapter 8) and utilised non-visual senses to locate prey.

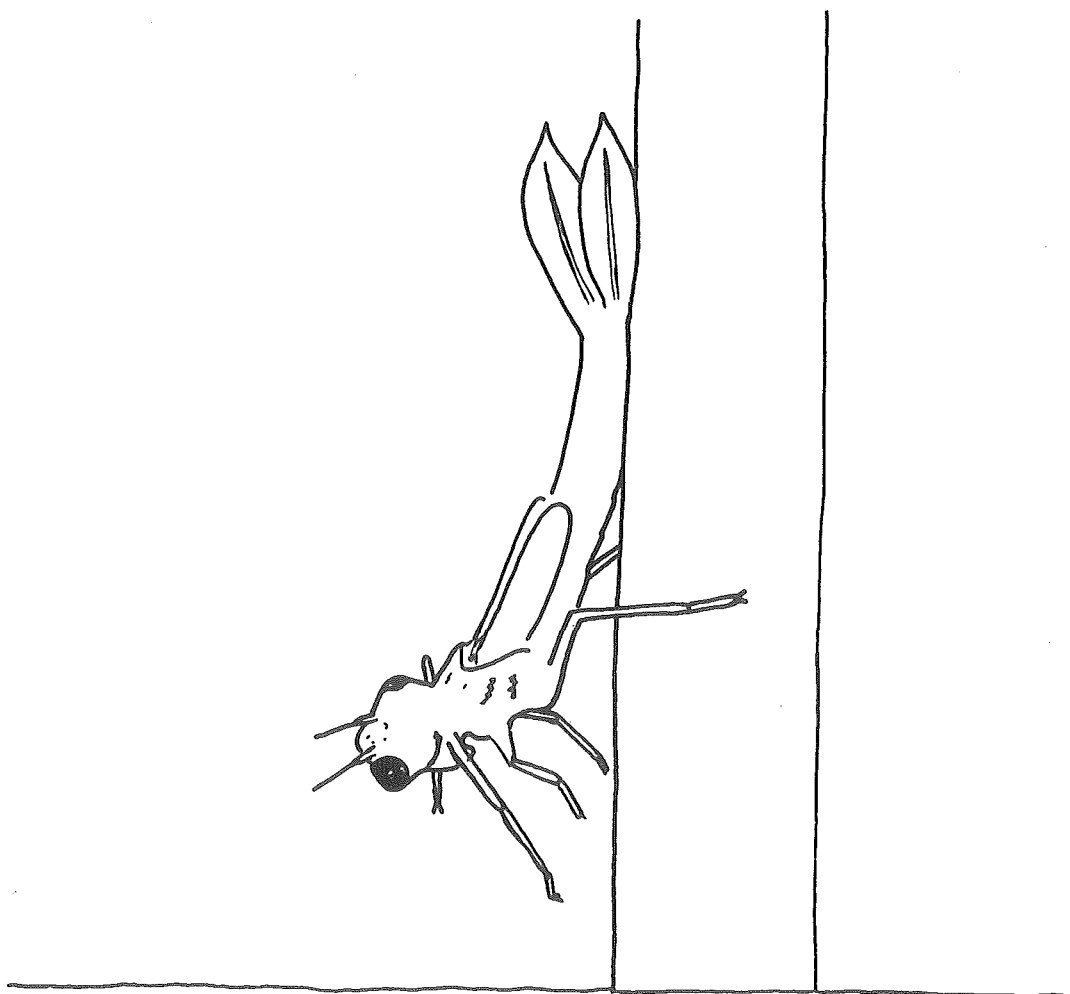


Fig. 27. Larva extending its attack range by reaching from stem.

Whereas larvae which were on the aquarium floor or perched head up on stems defaecated with their abdomens extended, larvae facing head down on perches curved their abdomens towards the aquarium floor before defaecating so that faecal pellets were deposited around the bases of occupied stems (Fig. 28). The quantity of faeces below stems with two occupants was compared with that found below stems occupied by a single larva over the same period of time. To allow sufficient time for the clearance of gut contents obtained elsewhere, only stems which had had the same occupants for more than 24h could be utilised in this analysis. Because of the instability of multi-occupied stems in the face of territorial behaviour (Chapter 2, 8), this condition was rarely fulfilled. Of 313 larval days monitored for faecal pellet production, only 22 occurrences (= 11 days) involved two larvae sharing a stem and only six of these were suitable for analysis (Table 15).

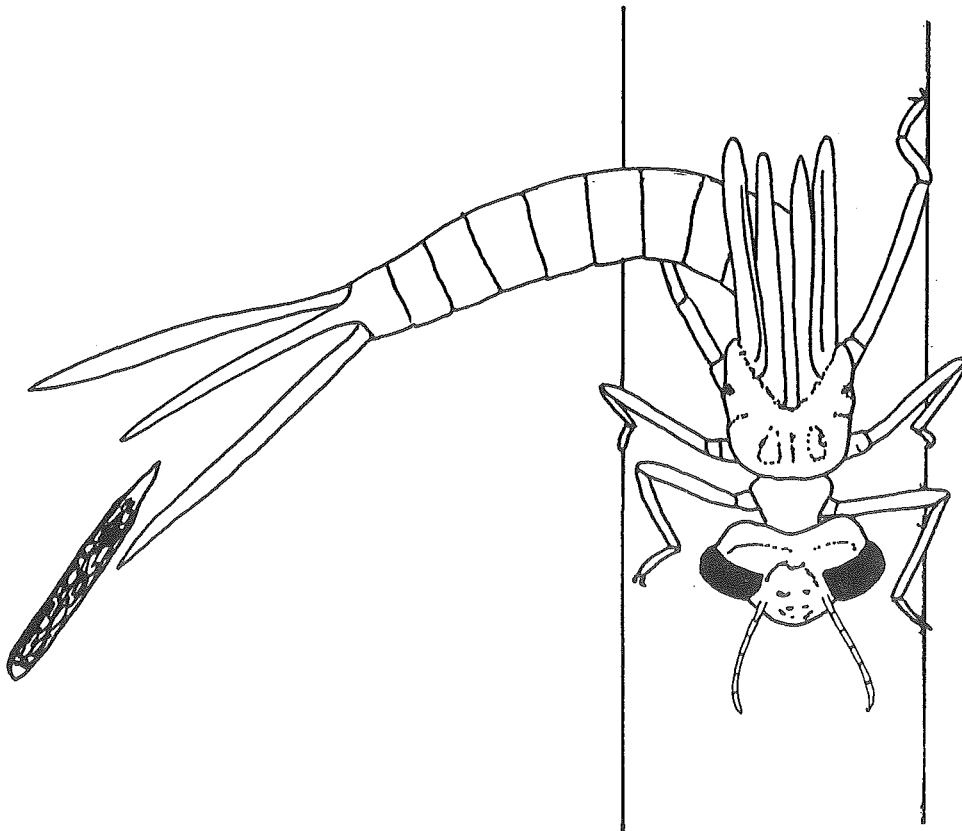


Fig. 28. X. zealandica larva defaecating from head-down position on stem.

Table 15. Faecal pellet production beneath stems with two larvae and stems with single occupants. The lengths of faecal material in each pellet are shown (in micrometer units, 1 micrometer unit = 0.64mm). The slash symbol separates the contributions of individual larvae.

date	two larvae	single occupants
1 - 3 Aug	7, 6, 5, 4, 4, 3	3, 1.5 / 4, 2, 1.5, 1 / 5, 3 / 5, 3 / 5
4 Aug	6, 5, 4, 2	5 / 3 / 6, 4, 2 / 3 / 5, 4, 4
7 Sept	6, 4, 2, 2	3 / 5, 3, 3 / 5
8 Sept	6, 5, 4	5, 3 / 6, 2 / 6, 4
9 Sept	5, 5, 4, 4, 2	4, 2 / 6 / 5, 3
10 Sept	7, 5, 3	4 / 5 / 5, 4

The data from 1 - 3 Aug and the data from 4 Aug were tested using the t-test for comparison of a single datum with a data set (Sokal and Rohlf 1981 box 9.7). Conditions in the aquarium from 7 through 10 Sept were considered to be uniform enough to justify use of an ANOVA, combining the data sets.

In all three cases there were significant differences between the rates of faecal pellet production (and presumably prey consumption) with two larvae on stems and that with a single larva. In the 1 - 3 Aug sample ($t = 11.98$, $p < 0.001$) and the 4 Aug sample ($t = 2.29$, $p < 0.1$), faecal pellet production from the two occupant stem was very much greater than twice the mean production below singly occupied stems (28.8 : 6.8 and 17 : 6.75 respectively). In the 7 - 10 Sept period there were again significant differences in faecal pellet production between the two cases (lengths of faecal pellets $F_{[1,14]} = 38.79$ $p < 10^{-4}$; numbers of faecal pellets $F_{[1,14]} = 24.58$ $p < 5 \times 10^{-3}$) but the mean length of faecal pellet larva⁻¹ day⁻¹ was about the same (8.0 (two occupants); 6.75(solitary larvae)).

Table 16. Numbers of each kind of prey found in faecal pellets of final instar X. zealandica collected at Cass pond on 5 occasions through the year. Dowdle (1981) examined diet at this site from December to April.

	Annelida				Insect larvae				Pupae	Other material		
	Number of larvae in sample	<u>Lumbriculus variegatus</u>	Lumbricidae	Other Oligochaeta	Crustacea	<u>Austrolestes colensoni</u>	Unidentified Zygotera	<u>Tanytarsus vespertinus</u>	<u>Chironomus* zealandicus</u>	<u>Gressittius* antarcticus</u>	<u>Gressittius antarcticus</u> pupae	
24 Sept	6	1	1	1	1	1	1	-	-	-/2	-	1x mite
5 Nov	32	7	2	9	11	1	-	3	7/3	2/9	1	1x <u>Gyraulus corinna</u> , <u>Physa acuta</u>
20 Nov	20	9	1	2	1	-	1	-	6/7	2/5	2	1x Ceratopogonidae
13 Mar	20	1	-	-	3	-	-	1	13/25	-/1	2	
13 Jun	22	-	-	-	2	1	2	-	9/8	-	-	1x compound eye
total	100	18	4	12	18	3	4	4	35/43	4/17	5	8
% numerical composition		10	2.3	6.8	10	1.7	2.3	2.3	20/24	2.3/10	2.8	4.5

* The solidus separates small ($\leq 1 \text{ mm}^3$) (on the left) from large ($\geq 3 \text{ mm}^3$) individuals.

The identified prey remains found in faecal pellets of final instar X. zealandica voided after collection are shown in Table 16. Laboratory observations showed that the handling time of prey in the size classes found in these faecal pellets was typically less than 2 min. Prey items as large as those recorded being scavenged (Chapter 5) would not normally be recorded in faecal pellets as characteristic parts (head capsules, mandibles etc.) are too large to enter the hypopharynx. General observations of X. zealandica larvae feeding in aquaria showed that with larger prey, head capsules and appendages were often lost during the feeding process.

DISCUSSION

The gut passage time found in the present study (mean = 10.5h, T = 16°C, prey = D. carinata) was shorter than the 15.2h (T = 15°C, prey = Daphnia magna Straus) calculated for similar sized larvae of Pyrrhosoma nymphula (Sulzer) (Zygoptera: Coenagrionidae) by Lawton (1971a). This difference was statistically significant at about the 5% level (Anderson-Darling Cramer-von Mises test, heuristic in Conover 1980). The biological significance, if any, of this difference is unclear. In Lawton's study, gut passage time ranged from about 6.5 to 24h whereas in X. zealandica it ranged from 6 to 18h. Lawton noted that insect prey produced a gut passage time approximately twice that found with Daphnia.

It had been my original intention to use the time (hour) of pellet evacuation to infer diel patterns in feeding in the field. Prey distribution at the time of maximal feeding might then have provided evidence of the actual microhabitats occupied in the field (Corbet 1962: 64) and information would have been obtained on the sensory mechanisms most commonly used in prey detection. Unfortunately, individual variation

proved to be too great to permit diagnostic use of gut passage times.

As Daphnia move about in mid water they might not be considered a 'good' prey with which to test for intraspecific interference, being, apparently, equally available to larvae at any position on a stem. Many of the prey items eaten in the field, however, also move in three dimensions, through the vegetation matrix of the littoral zone. A high proportion of prey eaten were relatively large, and would be expected to arrive within attack range in a random fashion. From the known gut passage time and the proportion of larvae with larger prey items among their gut contents it follows that large prey must frequently arrive within range. As prey capture and consumption time are short relative to time spent digesting prey, there would appear to be little or no advantage, from a feeding point of view, to the animal occupying the bottom of the stem (Chapter 8) in ejecting other animals (Chapter 2).

In this study the feeding regime in the laboratory, as measured through faecal pellet production, was similar to that in the field. Mean faecal pellet production per larva of animals 'sharing' stems in the aquaria was higher than that of lone occupants. Such a result is hard to reconcile with an interpretation of perches as defended hunting sites.

The gut contents of X. zealandica larvae have been examined in three previous studies (Crumpton 1979, Stark 1981, Dowdle 1981), and both Crumpton and Dowdle also recorded the proportion of animals having empty guts when captured. In a sample of 404 (mixed size) larvae taken over a year from Woodend pond (43°19'S, 172°42'E), Crumpton found 80.7% contained food remains in the foregut; whereas in a March sample of 146 larvae from Shipley's pond (43°28'S, 172°35'E) only 69% contained food. Dowdle found that 82.5% of 63 final instar larvae collected from the Cass pond in January and February produced faecal pellets. The results of the present study are consistent with her findings as 80% of all final instar larvae collected had food in their guts at the time of capture. Similar

results have been reported for other coenagrionid larvae (e.g. Pearlstone 1973, found that 75% of Enallagma boreale in monthly collections produced faecal pellets) and indicate that in the field larvae feed regularly.

There are marked divergences between the various accounts of X. zealandica diets from the field. My data indicates quite strong changes occur through time at the one site; this may account for discrepancies between this study and that of Dowdle (1981) who worked on the same pond. While neither Crumpton (1979) nor Dowdle (1981) found gastropod remains in field-caught X. zealandica larvae, they did occur in this study. Stark (1981) working on a lake population found Potamopyrgus antipodarum (Gray) (Gastropoda: Prosobranchia) was a major component of the diet of larger larvae. Non-arthropod prey remains (such as snail radulae) are very easily overlooked when examining faecal pellets. This study, Dowdle (1981) and Crumpton's Shipley's pond data produce a picture very similar to that found by Chutter (1961) for Pseudagrion, by Lawton (1970b) for Pyrrhosoma nymphula and by Thompson (1978c) for Ischnura elegans, of an animal with a diet based largely on Chironomidae. In contrast, Stark (1981) and Crumpton's Woodend pond data show a predator very dependent on utilising large numbers of small crustacea.

Estimation of food consumption rates from faeces production is difficult, the more so if the estimated food consumption rate is used to indicate a 'hunger' level. The behavioural responses of X. zealandica larvae indicate that even if they are feeding at below their maximal rate they are not necessarily under hunger stress.

X. zealandica larvae appear typical of 'sit and wait' predators. They remain on a site and attack passing prey when, or if, it becomes available. Prey from a broad taxonomic spectrum are taken and a high proportion of the food intake is from relatively large prey items (in the case of X. zealandica Chironomidae and Oligochaeta). While they are

competent predators on large prey, able to subdue and consume victims within a short time, they also capture and eat much smaller prey items, displaying considerable virtuosity in their repertoire of predatory behaviours.

The habit of starving larvae remaining on stems rather than pursuing food and the apparent absence of any advantage in predatory success for solitary larvae on stems casts considerable doubt on their value as 'fishing sites'. Given the effort put into defending these positions some alternative selective advantage for perches must be sought (Chapter 10).

Section 4: site selection and occupation

It has long been recognised that dragonfly larvae have preferences for different habitats (e.g. Tillyard 1917, Zahner 1959, Corbet 1957a, 1962, Johnson & Crowley 1980), although the mechanisms by which larvae establish these preferences are, in general, unclear. Dragonfly larvae are, in the main, restricted to habitats available in their natal water body, hence oviposition site selection is an important factor in determining the 'choice' available to larvae. In many (but not all) species, females are highly selective in their choice of oviposition site, responding to specific stimuli which (probably) correlate with the suitability as larval habitat (Corbet 1962, 1980). Some ostensibly aquatic dragonfly larvae can cross land but this perilous behaviour is probably expressed only when the natal water body has become uninhabitable.

For 'sit and wait' predators, those which have no searching component in their repertoire of predatory behaviours, perch site selection is a crucial component in the life history tactics. The perch site determines the microhabitat in which the animal lives, thereby establishing: the composition of the prey fauna available to the predator; the quantity and reliability of food access; the degree of intraspecific competition faced; the potential predators that will have to be avoided; the physical and chemical conditions in which it will develop and the range of climatic conditions to which it will be subjected. It is to be expected that different sites will have different utility values for the larvae.

Despite the preponderance of 'sit and wait' predators among arthropods there has been little work on their ecology. While an enormous literature exists on predation and predatory behaviour (reviews Curio 1976, Krebs et al 1983, Krebs & Davies 1978, 1984) this work has

concentrated almost exclusively on foraging or ambush predators. Contrary to a common usage, 'sit and wait' and 'ambush' are not synonymous but refer to different aspects of an animal's behavioural repertoire: 'sit and wait' refers to predator movement during prey localisation while 'ambush' refers to the method of prey acquisition. With the recognition that 'sit and wait' and ambush predators have an important role in ecosystems, and one distinct from that of foragers, there has been increasing interest in their activities and impact (Huey & Pianka 1981).

Investigations of the behaviour of arthropod 'sit and wait' predators have been concentrated on spiders (Araneae); among the insects mantids, larval Neuroptera (Myrmeleontidae), larval Coleoptera (Cicindellidae) and larval Trichoptera (Hydrophilidae) have been examined (Riechert 1978, Janetos 1982, Olive 1982, Rypstra 1982, Greenstone 1983, Holling 1966, MacKinnon 1970, Inoue & Matsura 1983, Wilson 1974, Griffiths 1981, 1982, Teramoto 1982, Boake et al 1984, Lucas 1985, Knisley & Pearson 1981, Formanowicz et al 1982). With some notable exceptions (Riechert 1978, Janetos 1982) most investigations have concentrated on short term phenomena. The long term aspect of site utilisation, implicit in the name 'sit and wait', has largely been overlooked. Amongst the insects examined this omission may be a consequence of short larval lifespan and observational difficulties. Many odonate larva are 'sit and wait' predators and, because they are easily maintained in the laboratory and, for insects, are long lived, they have the potential to be useful experimental subjects for investigating the parameters of 'sit and wait' behaviour in insects.

During larval development microhabitat requirements may change, necessitating changes in the kinds of sites occupied (e.g. Werner & Gilliam 1984). In a number of zygopteran species a slow drift of young larvae from the oviposition area to other habitats has been documented (Macan 1964, Lawton 1970a, Johannsson 1978). In other species the young

larvae disperse rapidly to new habitats (Johannsson 1978).

Tillyard (1917: p328) held that pattern of larval habitat preference correlated with taxonomic position at the family or subfamily level. Corbet (1960: p72) drew attention to the consistency of larval microhabitat preference within genera and more recently (Heymer 1973, Johannsson 1978, Johnson & Crowley 1980) further fine structuring of site selection has been demonstrated at the species level. As Corbet (1962: p47) stated with reference to functional morphology 'It is in the larval stage of Odonata that the greatest adaptive radiation ... has taken place'. While stated with anatomical adaptations in mind, this statement holds equally well for the behavioural components of morphology.

Among Coenagrionidae inter- and intraspecific differences in site preference have been demonstrated in ecological surveys and life history studies by Corbet (1957a), Chutter (1961), Macan (1964, 1965), Lawton (1970a), Pearlstone (1973), Johannsson (1978) and Johnson & Crowley (1980). Seasonal movement between habitats by coenagrionid larvae, with consequent changes in sites occupied, was found by Corbet (1957a), Macan (1964), Lawton (1970a) and Johannsson (1978). Whether such movements represent an adaptive response to north temperate winter conditions (i.e. the habitat change is important) or are the consequence of changing larval 'needs' during development (i.e. the site change is important) cannot in all probability be determined in the field (at least in temperate climes).

The only experimental examinations of site selection in odonate larvae appear to be those of Keetch & Moran (1966) on Paragomphus cognatus (Rambur) (Anisoptera: Gomphidae), Prodon (1976) on Cordulegaster boltoni (Donovan) (Anisoptera: Cordulegasteridae) and Kime (1974) on Aeshna californica Calvert and Anax junius Drury (Anisoptera: Aeshnidae). Both Paragomphus and Cordulegaster are burrowing species and habitat selection is strongly influenced by

substrate particle size and current. A. californica is a 'sit and wait', ambush predator and perch diameter has an important influence on site selection, whereas A. junius is an active forager and is little influenced by substrate geometry.

Despite the recognised importance of site selection among Zygoptera and the suggestion that, in the absence of predatory fish, Zygoptera may displace Anisoptera species (Johnson & Crowley 1980), no experimental work appears to have been done to find factors which affect site selection among Zygoptera.

X. zealandica larvae are territorial (Rowe 1980) and have a rich and extensive repertoire of agonistic displays (Chapter 2). The elaborate system of displays and the time spent defending perching sites (with its consequent opportunity cost vis a vis feeding) would indicate these sites have some major significance in the life history of the animals. The expenditure of time and effort to defend a particular site is easily explicable (at least at a superficial level) when there is a heavy 'engineering' investment at that place (e.g. spider webs, burrows etc.) or when resources are distributed in small rich patches so as to be economically defendable (Wilson 1975). However, since X. zealandica larvae have the capability to be highly mobile, make no investment in site modification and utilise a variable but apparently superabundant food source the defence of a territory is difficult to explain, the more so when sites also appear superabundant under most circumstances.

There has been speculation on the adaptive significance of the sites occupied by dragonfly larvae. The conventional wisdom has been that the sites occupied function primarily as 'fishing sites' (e.g. Macan 1977, Thompson 1978a, Crowley 1979, Lawton et al 1980, Baker 1980, 1982) but the results of Chapter 6 do not support this interpretation insofar as X. zealandica is concerned. The demonstration of spatial separation of larval cohorts within a single species in the field (Corbet

1957a, Lawton 1970a, Johannsson 1978) has been interpreted in terms of resource partitioning as proposed by Hutchinson (1959). An alternative view, based on Corbet (1957b), that larger conspecifics are the potential predators most consistently present, and, therefore, behaviours which reduce intercohort contact have adaptive value to smaller individuals, also has supporters. In the absence of experimental investigations, this set of hypotheses should not be regarded as exhaustive.

In the chapters of this section I examine site use by second instar larvae (the first free living stage) and the influences of site geometry, prey regime and developmental state on site usage by larger larvae.

CHAPTER 7

Site occupation by young X. zealandica larvae

INTRODUCTION

Almost nothing is known of the activities of dragonfly larvae during their first 6–8 instars, despite the fact that in many species half the lifespan passes in these stages. Richard (1961) and Caillere (1974) briefly examined predatory behaviour of the early instars of Calopteryx virgo (L.) and Calopteryx splendens (Harris) (Zygoptera: Calopterygidae). The predatory behaviour of the second instar of Xanthocnemis zealandica (McLachlan) (Zygoptera: Coenagrionidae) has also been examined (Chapter 4). Corbet (1957a), Macan (1964), Lawton (1970b) and Johannsson (1978) examined distribution within habitats of early instars of several coenagrionid species (Coenagrion mercuriale (Charpentier), Ceriagrion tenellum (Villers), Pyrrhosoma nymphula (Sulzer), Enallagma cyathigerum (Charpentier), Coenagrion pulchellum (vanderLinden), Ischnura elegans (vanderLinden), Erythromma najas (Hansemann)). In general the small size and cryptic behaviour of young dragonfly larvae has made them an unappealing experimental subject.

In this study I established the site usage pattern of second and third instar X. zealandica in the laboratory. This pattern was compared with those of young Xanthocnemis sobrina, Ischnura aurora (Zygoptera: Coenagrionidae) and Procordulia grayi (Anisoptera: Corduliidae) held under the same conditions.

METHODS

Ovipositing tandem pairs of X. zealandica (McLachlan) and X. sobrina (McLachlan), and ovipositing females of Ischnura aurora (Brauer) and Procordulia grayi (Selys) were collected and induced to lay in the laboratory (Rowe in press). Ova were maintained indoors at about 20°C until hatching occurred. Recently emerged second instar larvae (in Odonata the first larval instar is a specialised non-feeding stage which typically lasts only a few minutes - see Corbet (1962)) were introduced into the experimental containers and their behaviour monitored. Experimental containers were 5-cm diameter Syracuse dishes with ten 2 x 2 mm cardboard squares glued ('Selleys' PVA) in two rows (rows 10-12 mm apart; individual squares 4-6 mm apart) to the bottom and allowed to dry for at least seven days. Ten sites were offered to reduce the probability that larvae abandoning then reoccupying their original position would generate false records of apparent site fidelity. Prior to the ova hatching, copepods from a culture of Phyllognathopus volcanicus Barclay (a known prey of early instar X. zealandica) were added to each dish and additional water was added to produce a maximum depth of 4 mm at the centre of the dish. Two or three days later a single, newly hatched larva was introduced to each container and its behaviour was monitored. At least 10 (and up to 25) 'replicates' were maintained throughout an experimental run. All larvae in a run came from the same egg batch and were kept under 'room conditions' (about 16h light: 8h dark, temperature 18-23°C).

Locations of larvae within a Syracuse dish were noted at regular intervals. At different times, three sampling protocols were used - 4h intervals (8AM, noon, 4PM and 8PM) during the day; thrice daily (9AM, noon, 9PM), or daily (at noon). All sampling schemes resulted in both left and right censoring of data, but it was not practical to avoid this.

Often it was necessary to use a hand lens to find larvae, even those still occupying the same, known, site.

To ameliorate difficulties caused by the right censoring inherent in the sampling scheme and bias introduced by long gaps in the record over night hours, analysis of duration of occupation was carried out on the cumulative function. The cumulative function was generated simply by summing all occupations which survived any given time. Cumulative and integrated functions tend to be stable because they damp the fluctuations caused by 'noise' (an explanation for the use of this procedure is given in Appendix 1).

To allow comparison with the behaviour of other species, 2nd instar larvae of X. sobrina, I. aurora and P. grayi were also examined under the same conditions as those of X. zealandica. Some X. zealandica, X. sobrina and I. aurora larvae were raised to later instars and were observed to obtain information on the ontogeny of site occupation.

RESULTS

Water depth was an important factor affecting larval behaviour. When depth at the dish wall was greater than 2 mm, larvae moved onto the sides of the dish immediately below the meniscus. However, if the water depth was maintained at a lower level larvae remained on the floor of the dish and colonised the cardboard squares. Data presented are for shallow water conditions.

The time spent in the second instar ranged from 6 to 14 days. The duration of the instar was probably dependent on temperature and food regime as larvae raised at the same time had similar development patterns (e.g. batch 1 duration 12-14 days, $n = 6$; batch 2 duration 6-9 days, $n = 7$). Only larvae from batch 1 were used through the third instar (duration 10-12 days, $n = 4$).

Occupation time v frequency data in all cases had means approximately equal to the standard deviation, indicative of a negative exponential distribution. The cumulative frequency data is presented as semi-log plots (Figs 29–31). With second instar X. zealandica larvae regression of \ln (cumulative frequency) against duration of occupation produced a good fit (Pearson's r typically > 0.98).

The use of cardboard squares in contrast to other sites was examined on a regular basis (Table 17). In the series of dishes observed using the 4h sampling scheme larvae appeared to be localising at spots on the floor. There was no statistically significant variation ($P > 0.05$) detectable between the duration of localisation on the floor and that on cardboard squares (mean(floor) = 16.8h, S.D. = 11.7 ($n = 30$);

Table 17. Use of cardboard squares as perch sites by X. zealandica larvae in the 2nd and 3rd instars.

Three sampling schemes were used: scheme 1 involved daily examination at noon; scheme 2 involved 3 examinations per day and scheme 3 involved examinations at 4h intervals. The total number of observations of larvae on the cardboard perches provided ('on') is contrasted with the maximum possible number of occupations (= total number of observations of live larvae) and given as a percentage.

experiment identifier	on	maximum possible	as %
2nd instar (scheme 1)	69	90	77
2nd instar (scheme 2)	32	46	70
2nd instar (scheme 3)*	44	126	35
3rd instar (scheme 1)	68	85	80

* This anomalous result in the 2nd instar 4h sampling period experiment is discussed in the text.

Table 18. Use of cardboard squares as perch sites by young X. sobrina larvae. Site use examined at noon daily. Conventions as in Table 17.

experiment identifier (= instar examined)	on	maximum possible	as %
second	11	78	14
third	6	8	75
fourth	19	24	79
fifth	18	25	72
sixth	36	49	73

Table 19. Use of cardboard squares as perch sites by young I. aurora larvae. Site use examined at noon daily. Conventions as in Table 17.

experiment identifier (= instar examined)	on	maximum possible	as %
second	5	12	42
third	6	11	55
fourth	5	14	36
fifth	10	18	56

mean(squares) = 15.0h, S.D. = 14.3 (n = 31)). This experiment was run using pre-used Syracuse dishes and larvae appeared to be localising on patches of vegetable matter on the floor of the container.

The single experiment with 3rd instar X. zealandica larvae produced a result which had a markedly inferior fit to a simple exponential (Fig. 32).

X. sobrina larvae were probably being held near their thermal threshold during these experiments (Chapter 1.). Second instar larvae did

Figs 29–31. Pattern of occupation of cardboard squares by second-instar X. zealandica larvae. The total number of occupations which lasted at least the given number of hours is plotted as a semi-log graph against the duration of occupation. The advantages of using the cumulative frequency, rather than raw data, are outlined in Appendix 1.

The least squares fitted regression line to the log data is given. The slope of this line is a measure of the exponential decay constant.

Fig. 29. Durations of occupation found when sampling daily (scheme 1).

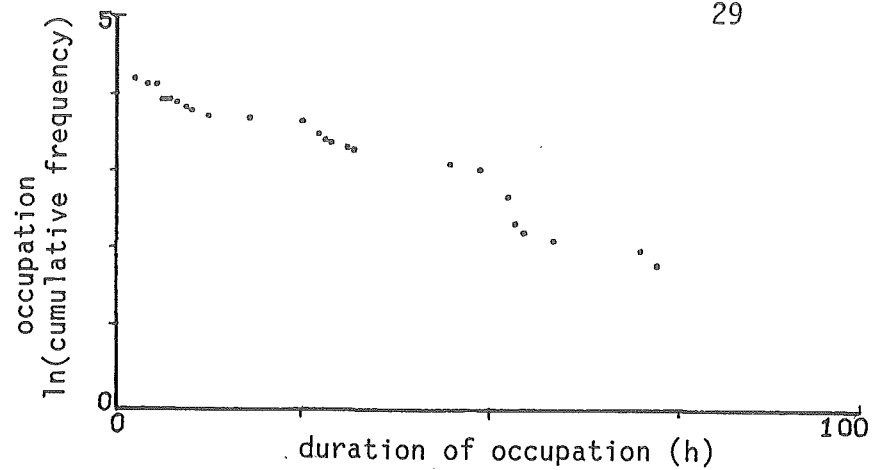
$$\ln(\text{cumulative frequency}) = 3.09 - 0.016 \times \text{duration}; r = -0.99$$

Fig. 30. Durations of occupation found when sampling 3x daily (scheme 2).

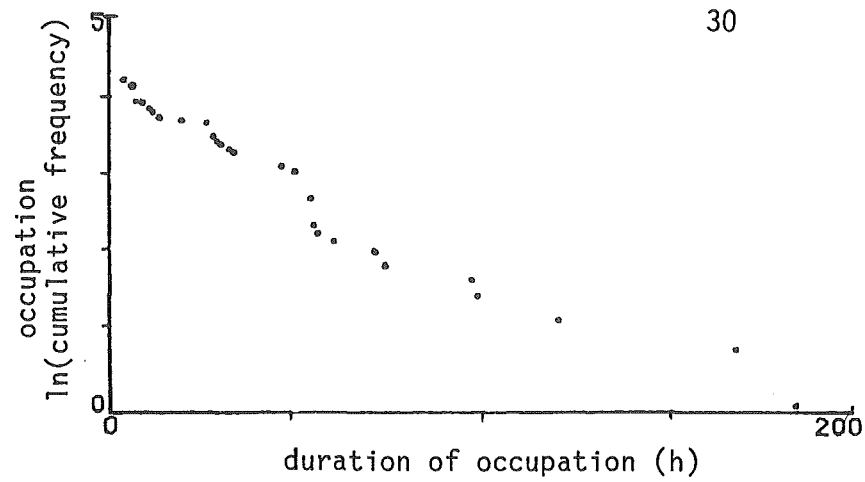
$$\ln(\text{cumulative frequency}) = 3.92 - 0.023 \times \text{duration}; r = -0.97$$

Fig. 31. Durations of occupation found when sampling at 4h intervals (scheme 3).

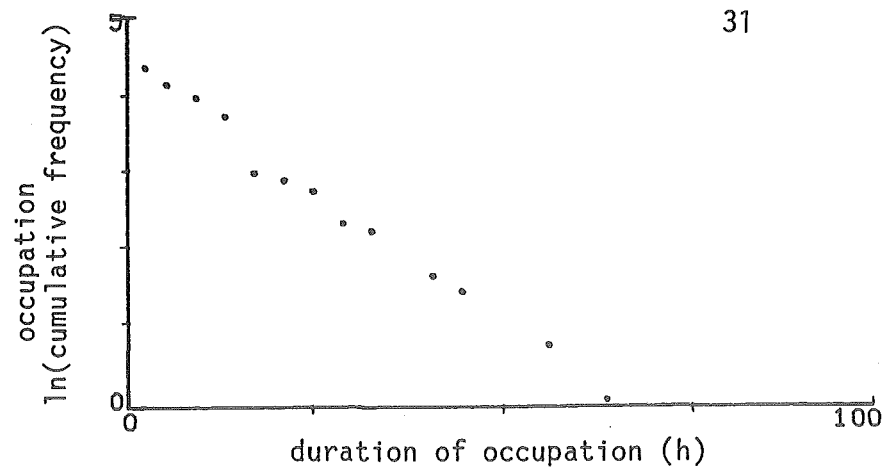
$$\ln(\text{cumulative frequency}) = 4.31 - 0.67 \times \text{duration}; r = -0.995$$



30



31



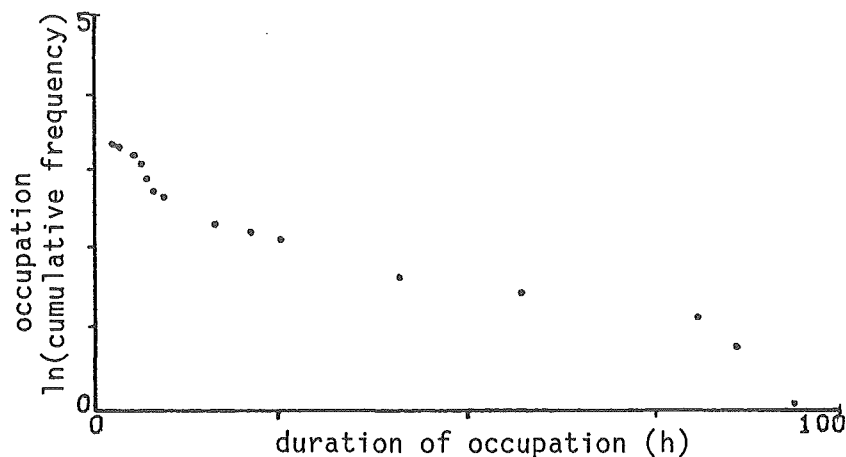


Fig. 32. Pattern of site occupation by third instar X. zealandica

larvae. Conventions as for Figs 29–31. Least squares fitted line:

$$\ln (\text{cumulative frequency}) = 3.0 - 0.029 \times \text{duration}; r = -0.968$$

not localise on the cardboard squares provided (Table 18.), but wandered on the floors of the Syracuse dishes. Later instar larvae occupied the cardboard squares and often remained on the one site for many days.

I. aurora larvae were never observed to occupy any cardboard square for more than 24h, but even so they were often on the squares (Table 19.). In contrast, P. grayi were observed on cardboard squares on only 16 of 84 possible occasions and never remained for more than a few hours.

DISCUSSION

Young X. zealandica larvae had a strong propensity to localise on the cardboard squares which comprised only 2% of the bottom area of the dish. This localisation was the more impressive when it is considered that the parameters determining site preference are largely undetermined and that small cardboard squares are unlikely to be the most attractive sites to these small larvae. The vertical surfaces of the dish walls were

preferred when they were habitable, and cardboard squares and vegetable matter on the dish floor appeared to have approximately equal attraction.

Different experimental runs with second instar X. zealandica produced semi-log frequency v duration graphs with markedly different gradients, indicating different patterns of site fidelity. Despite the difference in time spent in the second instar by larvae in scheme 1 (about 312h) and those in scheme 2 (about 170h) their patterns of site occupation were similar. In contrast, larvae in scheme 3 also had an internally consistent pattern of site occupation but (Fig. 31) this differed from that found in the other two experiments. The gradient of a log-linear graph is usually a good approximation to the exponential decay constant and the occurrence of internally consistent, but mutually incompatible, decay constants is, for the moment, inexplicable.

The 'halflives' of site occupation by second instar X. zealandica larvae of batches 1 and 2 and of the third instar larvae of batch 1 were approximately 30-35h. When compared with the total durations of these larval instars (about 312, 170 and 264h respectively) the sedentary nature of X. zealandica larvae is apparent.

After the second instar (which may have been under stress), X. sobrina larvae displayed a similar pattern of site usage to X. zealandica. In contrast, while I. aurora larvae did occupy the cardboard sites quite frequently, they did not display the site fidelity apparent in the Xanthocnemis species. P. grayi failed to use the sites offered. The differences in behaviour between the species would indicate that the observed site utilisation patterns are not simply a consequence of the surface qualities of the cardboard squares.

The contrast in site usage between X. zealandica and I. aurora (Chapter 2) was established from the earliest free living stages. X. zealandica adopts a sedentary life style from the beginning of its larval life.

CHAPTER 8

Site selection, occupation and use by X. zealandica larvae

INTRODUCTION

Despite the almost self evident importance of the sites occupied to the life-history tactics of sit and wait predators, remarkably little is known of the factors influencing site choice either in Zygoptera larvae (Corbet 1962, Crowley 1979, Thompson 1982) or in other arthropod predators (e.g. Riechert 1978, Janetos 1982, Heinrich & Heinrich 1984). Field studies on coenagrionid larvae (e.g. Thompson 1978c, 1982) have been hampered by the absence of information on where these predators go and what they do. Direct observation of coenagrionid larvae in the field is almost impossible and previous laboratory studies have not addressed themselves to the problem of site occupation and usage. An understanding of the underlying patterns of site selection and usage by coenagrionid larvae must help shed light on the effects these often extremely abundant predators have within aquatic communities.

When this study commenced there was no information on which variables might prove to be important in influencing the behaviour of X. zealandica larvae, as there had been no previous experimental work on site selection and usage by zygopteran larvae. Therefore, investigations were designed around the initial assumption that for any given substrate geometry, larvae would adjust their positions in response to prey availability. Larvae were expected to select different sites when prey with different behaviours were present, as suggested by Macan (1964, 1977), Crowley (1979), Lawton et al (1980), Thompson (1982) and (implicitly) by Baker (1980, 1982). This proved not to be the case.

In this study I examined the effects of stem diameter and age on site selection preferences; the influence of site structure on occupation patterns and the influence of events such as moulting and metamorphosis on site usage. Changes in site occupation behaviour due to larval ontogeny, diel activity patterns, prey type, larval density effects and intraspecific interactions were sought.

METHODS

Standard aquaria (25 x 40 x 15 cm deep) were filled with water to a depth of 10–12 cm, placed in a 16°C controlled temperature room under a 16h light/8h dark regime and allowed to stand for 48h. Stems and other substrates were then added. Substrates (other than artificial plants) were produced from Feltex Rubber (Plastics Division) 'non toxic' PVC tubing with 2-, 4.5-, 7-, 9- and 11-mm outside diameter. The 2-mm tube was stiffened with thin wire; 4.5-, 7- and 9-mm stems were stiffened with brazing rod and the 11-mm tube was slipped over a 4.5-mm stem. Stems were made up in frames. Each frame consisted of a 1.5 cm square wooden bar about 50 cm long with a line of 4 holes drilled through it, about 6 cm apart. The metal stiffener (wire or rod) could slide freely within these holes to ensure stems reached the bottom of the aquarium. Metal stiffeners were bent at right angles to permit the stems to be rotated so larvae 'squirrelling' about stems or in the cryptic posture could be found.

In addition to stems and facsimile plants, 'trees' (stems with 3 cross branches impaled through them at 2.5–3 cm intervals), 'leaves' (polyethylene sheet attached to the branches of 'trees') and 'roots' (lengths of stem lying in the bottom of the aquarium) were used to provide a variety of sites.

Space limitations in the constant temperature, controlled light room (conditions needed to maintain larvae in their diapause state

(Deacon 1979)), meant it was possible to operate only 12 aquaria at any one time. Once diapause was broken, larvae underwent metamorphosis and emerged within a few weeks.

Stem colonisation investigations

X. zealandica larvae were reluctant to colonise freshly prepared plastic stems, but this effect passed after stems had been in water for a few days. All experiments other than those designed specifically to investigate the effect of stem 'age' were conducted using stems which had been held for at least seven days in an aquarium.

At the beginning of an experiment, larvae were added to the aquarium. Eight animals at a time were used when investigating the behaviours of final and penultimate instar larvae and 20 animals when investigating larvae in instars 6-9. The larger number used when examining the behaviour of smaller larvae was to compensate for their propensity to sit on the walls or floor of the aquarium, or on small pieces of debris rather than on the stems provided.

Each aquarium was examined 1, 24 and 48 hours after the introduction of the larvae and the perch occupation pattern was recorded. After 48h the rear row of stems was moved to the front of the aquarium and the larvae were shaken from the stems to begin a new experimental cycle. Because of the territorial defence behaviour of the occupants (Chapter 2) this protocol introduced a systematic bias against finding a preference. During colonisation experiments the cladoceran Simocephalus exspinosus (Koch) was provided as prey. Aquaria were restocked with prey whenever prey numbers declined.

Larvae with access to 11-mm diameter stems often occupied either the stiffener support within the stem or the sharply curved boundary at the end of the stem. These larvae were not classed as occupying the stems.

Results were tested for significance against the tails of the binomial distribution assuming no preference was exhibited.

Site usage investigations

Larvae were marked individually with fluorescent plastic leg rings (Rowe 1979) before being released randomly, into an aquarium. Observations were made in a 'free range' situation where larvae were allowed to distribute themselves through the available habitat. The position and orientation of every larva was recorded regularly. Monitoring 'scans' were made every 24h at 'noon' (room light cycle time). In addition, an intensive monitoring programme, involving hourly or bihourly 'scans', was conducted at irregular intervals to check for short term behavioural changes which would have invalidated the regular sampling programme. None were found. Typically, larvae were followed for 1-2 months under each experimental treatment and then conditions were changed. Surviving larvae were followed until emergence (6-8 months in some cases). This method results in a lack of independence of individual observations, making statistical comparisons difficult; but it does provide a measure of site utilisation over a long time scale, permitting the detection of patterns which would not be apparent in frequently disturbed systems. Further constraints were imposed by the need to allow larvae to 'settle' for some time to obviate the effects of handling and the need, where possible, to compare treatments in the same aquarium to standardise conditions of prey type and availability.

For the main series of experiments, 8 larvae and 8 stems were used in each aquarium. In experiments to investigate density effects, standard aquaria were set up to provide a range of larval/stem densities.

Larval site selection behaviour had every appearance of being a simple, regular Markov process (Daellenbach et al 1983). In such a situation the system will approach its unique steady state independent of the details of the starting position as time progresses and the effects

of the initial conditions wear off. Initial conditions can be expected to vary widely as larvae would be under considerable stress at the time of their introduction to an aquarium. The duration of an experiment needed to be very much longer than the 'relaxation time' of the system to allow the system to settle.

Observations made in a single aquarium suffered from a high degree of correlation in site use through time. However, as time approaches infinity the cumulative distribution should approach the steady state distribution (if one exists). Real observations are restricted by the finite length of observation time available, the more if, as in the present study, the duration of an individual site occupation by a larva is of the same order as the total observation time.

Because observations are not independent, frequencies cannot be compared using a Chi-square (or similar) test (see Hurlbert 1984: p205-6). It is possible to treat the populations from each aquarium as independent estimates of the steady state and to use ANOVA or Mann-Whitney U-tests. However, Hurlbert (1984) cautions that such analyses are weak.

Diel activity patterns. Diel movements of larvae were examined in three aquaria into which larvae had been introduced 2-4 weeks before. This long waiting period was used to minimise stem colonisation movements. Aquaria were maintained at 16°C under a 12h light: 12h dark regime. Each aquarium held 8 final instar X. zealandica larvae in diapause and 8 plastic stems (4.5-mm diameter). Aquaria were examined 7 times each night, at hourly intervals, starting 1h after 'lights out'. Observations were made under dim red light (household torch with photographic '25A' filter taped over the beam). During the day the same aquaria were examined 7 times, at hourly intervals, starting 1h after 'lights on'. The exact position of each larva was noted at each observation time and any change of position was recorded as a 'movement'. To minimise the influence of observer

movement, larval activity was monitored in only one aquarium during any one 24h period. The hourly sampling rate was very much higher than the 'normal' time scale of X.zealandica larval activity.

Moulting. The data set from each standard aquarium 'set up' was scanned and the locations and orientations of all moulting larvae for the 2 days prior to and the 2 days immediately after ecdysis were abstracted. Only moulting larvae which had been alone on a perch on at least one day before and one day after moulting and which survived ecdysis by 48h were included in subsequent analyses. This protocol was chosen because larvae sharing perches would have been subject to the effects of agonistic interactions and the behaviour patterns of dying larvae were probably 'abnormal'.

Emergence. The data set from each standard aquarium 'set up' was scanned and the locations and orientations of all emerging larvae on the last 10 days of aquatic life were abstracted. Only emerging larvae which had been alone on a perch for 7 of the last 10 days, alone on the last day and on one other of the last 3 days were included in the analysis. The 10 day 'window' was set in light of Deacon's (1979) observations on metamorphosis in X. zealandica at 16°C; the 'lone occupant' requirement was chosen to limit the potentially confounding influences of intraspecific agonistic interactions.

Prey. To test the potential effects of prey availability on site selection several of food regimes were used: no food, lumbriculid worms, mosquito larvae and two cladoceran species (Daphnia carinata King, Simocephalus exspinosus (Koch)). The prey species provided a range of behaviours of the kinds displayed by the natural foods of X. zealandica (Chapter 6). The lumbriculids moved across the aquarium floor and entwined themselves at the bottom of stems; the mosquito larvae

moved across the aquarium floor while feeding and also swam actively in the water column; D. carinata remained in midwater whereas S. exspinosus moved across leaves and other surfaces.

Cladoceran prey species were maintained in laboratory culture. Mosquito larvae were Opifex fuscus (Hutton) obtained from the Edward Percival Field Station at Kaikoura and the lumbriculid worms were Lumbriculus variegatus Muller obtained from a fish food stockist. Attempts were made to use chironomid larvae but I had difficulties obtaining a consistent supply of appropriately sized prey.

X. zealandica larvae were held in an aquarium with a given prey species for several weeks and were then transferred together with their sites to another aquarium. Site occupation and usage of the X. zealandica larvae under the different prey regimes were compared.

Density effects Final and penultimate instar larvae were presented with 4.5-mm stems. With 8 stems provided, 1, 4 or 16 larvae were placed in an aquarium, with 4 stems, 4 or 8 larvae; and with 16 stems, 8 or 16 larvae. These regimes provided a range of densities in terms both of per m² and per stem, the two most natural density measures for this species.

Intraspecific interactions. The data set from each standard aquarium 'set up' was scanned and the locations and orientations of all larvae which were on perches with more than one occupant were recorded.

Comparison with Austrolestes colenonis

Larvae of A. colenonis were placed in standard aquaria with either 4.5-mm or 11-mm stems and were monitored daily for 7-20 days, as for X. zealandica. Four 'runs' were made, each using 8 penultimate or antepenultimate instar larvae.

RESULTS

Stem colonisation investigations

Experiments run with larvae collected at the same time produced consistent results but larvae from different collection dates sometimes behaved in markedly different ways. In contrast to the long term experiments where larvae displayed a very high rate of stem occupancy during stem colonisation experiments all larvae did not necessarily manage to occupy a stem within the time allowed. This lowered the rate of data acquisition. With the final and penultimate instar larvae this problem could not be solved by increasing the density because the territorial behaviour would drive 'excess' larvae onto the less preferred sites.

Experience of larvae A preliminary investigation showed that larvae with previous experience of plastic stems appeared to colonise such sites more quickly (Fig. 33). Consequently, all preference experiments were carried out using larvae which had been allowed to utilise plastic stems for at least a week in a holding aquarium.

'Age' of stems When larvae were given a choice of 'fresh' or 'aged' stems there was a slight preference for the 'aged' stems. After 48h, 16 larvae were on 'aged' stems and 8 on fresh stems ($P(\text{indifferent}) < .15$, two tailed binomial). While this 'preference' was of low statistical significance, care was taken that all experiments were run using 'aged' stems to avoid possible systematic bias.

Stem diameter effects When larvae were presented with potential perches of different diameters, strong preferences were displayed in most cases (Table 20) and it was apparent that larvae were not indifferent to differences in stem diameter. In the case of 11-mm vs 4.5-mm stems anomalous results were obtained. Larvae collected during the summer showed a consistently strong preference for 4.5-mm diameter stems whereas

Table 20. Stem diameter choice by final and penultimate instar X.
zealandica larvae.

Larvae were offered 8 stems of each of two different diameters. The number of larvae on stems of each diameter were recorded at 1, 24 and 48h. After 48h all larvae were removed from stems and the experiment was restarted. This table contains the accumulated distributions (at 48h) for several runs with the same larvae. Probability values (2-tailed) obtained from a binomial distribution assuming no preference.

Stem pair tested		Distribution		P(indifferent)
1st	2nd	1st	2nd	
2-mm	4.5-mm	65	146	$<10^{-5}$
2-mm	7-mm	9	37	$<4 \times 10^{-5}$
2-mm	9-mm	23	57	$<2 \times 10^{-3}$
2-mm	11-mm	29	65	$<2.6 \times 10^{-4}$
4.5-mm	7-mm	26	28	$<.89$
4.5-mm	9-mm	29	4	$<1.1 \times 10^{-5}$
4.5-mm	11-mm	54	13	$<4.5 \times 10^{-7}$ (summer larvae)
4.5-mm	11-mm	7	12	$<.36$ (wintering larvae)
7-mm	9-mm	37	27	$<.26$

those collected at or after the autumn equinox had a marked preference for the larger, 11-mm diameter stems.

The proportion of larvae occupying stems of different diameters, together with appropriate 95% confidence intervals, are presented in Figs 34-39. These show the ratio of larvae on reference diameter stems to total larvae on stems. Fig. 34 indicates a preference for 4.5-mm diameter stems. The marked consistency in site selection, except in the case of the post equinoctial sample, should be noted.

The infinite diameter contrast (Fig. 34) was obtained from the overall occupancy rate of 4.5-mm diameter stems in the long run aquaria. This represents a lower limit estimate, since in making calculations all

larvae off stems have been treated as if they were occupying sites on the aquarium walls; this was not the case as some were moving about on the floor and walls and were not localised on a site. Figs 35-39 present cumulative results of experiments summarised in Table 20; the 0.5 values of preference, logically necessary when a given diameter was compared with itself, have been given nominal confidence intervals (dashed) for a sample size of 100. This provides a visual comparison with the experimental data, of necessity obtained from samples of finite size.

During the course of these experiments, larvae were free to change their perches. When site occupation at 1, 24 and 48 h was compared, a slight, statistically non-significant, but perhaps biologically meaningful, change could be seen. Larvae offered 4.5-mm stems and either 2-mm or 9-mm stems moved onto the 4.5-mm stems, whereas those choosing between 4.5-mm and 7-mm stems showed no consistent preferences.

Early instar larvae (6 - 9)

The site diameter preferences of small larvae (headwidths 1.1 - 1.93 mm, putative instars 7 - 9) are shown in Figs 40-43. It was apparent that larvae in this instar range discriminated less between stems of different diameter than final and penultimate instar larvae tested, but nevertheless the general pattern of site preference was similar.

Ontogenetic changes. The preference for 4.5-mm as opposed to 2-mm stems is shown as a function of headwidth in Fig. 44, and is reinterpreted in Fig. 45 in terms of putative instar. Very little change, and certainly no biologically significant change, occurs after the eighth instar. On the other hand, the smallest larvae examined, those in the sixth (and seventh) instars, displayed a marked preference for small diameter (2-mm) stems.

Fig. 33. Effect of larval experience on time taken to colonise stems.

Eight larvae were released (at $t = 0$) in an aquarium with 16 stems. Larvae with previous experience of stems (symbol \cdot , 3 replicates) took appreciably less time to occupy stems than did naive larvae from the field (symbol x , 2 replicates). The number of larvae on stems is plotted against $\ln(\text{elapsed time})$.

Fig. 34. Stem diameter preference in final-instar X. zealandica larvae.

Eight larvae were held for 48h in an aquarium with 8 x 4.5mm diameter stems and 8 stems of another diameter. The graph shows the proportion of larvae on stems that occupied the 4.5mm diameter stems (see text). The 95% confidence intervals are indicated.

Fig. 35. Stem diameter preference in final-instar X. zealandica larvae.

Eight larvae were held for 48h in an aquarium with 8 x 2mm diameter stems and 8 stems of another diameter. The graph shows the proportion of larvae on stems that occupied the 2mm diameter stems (see text). The 95% confidence intervals are indicated.

Fig. 36. Stem diameter preference in final-instar X. zealandica larvae.

Eight larvae were held for 48h in an aquarium with 8 x 4.5mm diameter stems and 8 stems of another diameter. The graph shows the proportion of larvae on stems that occupied the 4.5mm diameter stems (see text). The 95% confidence intervals are indicated.

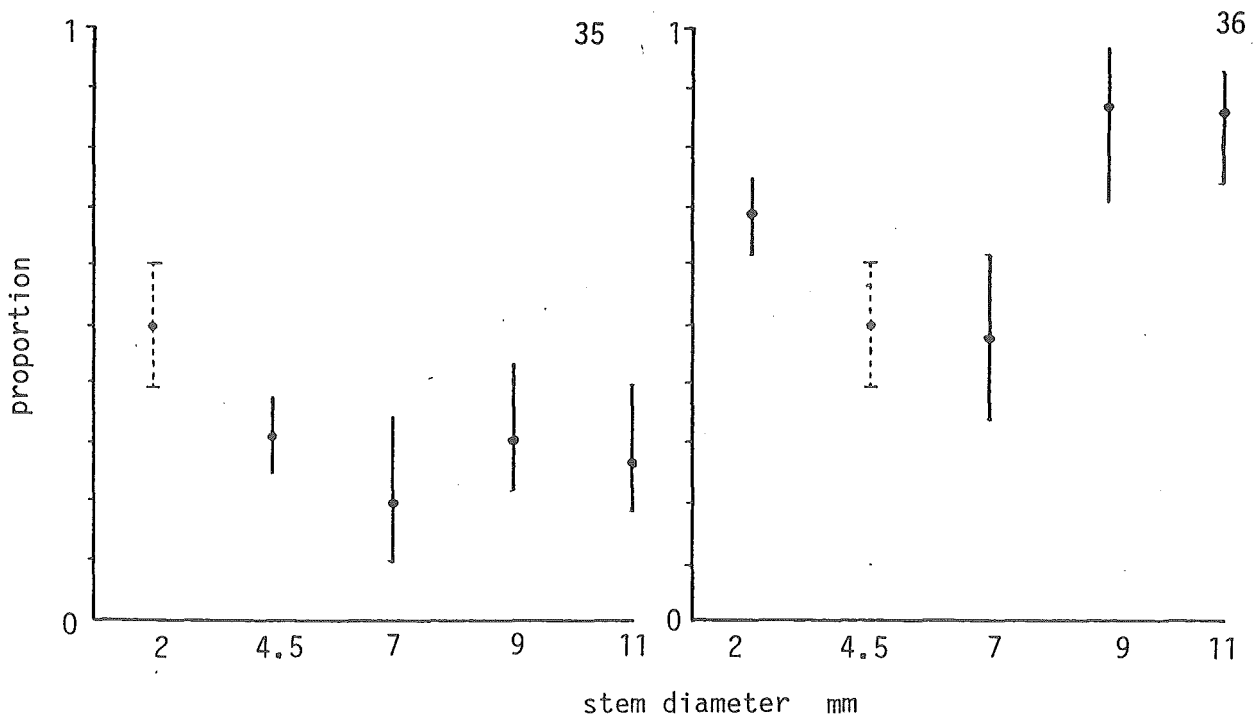
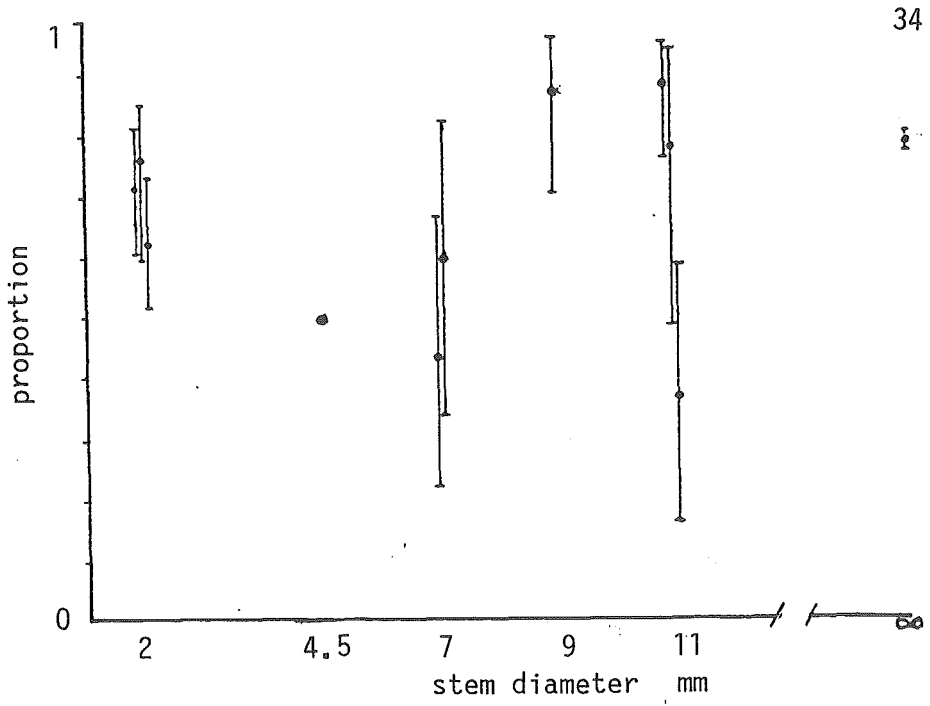
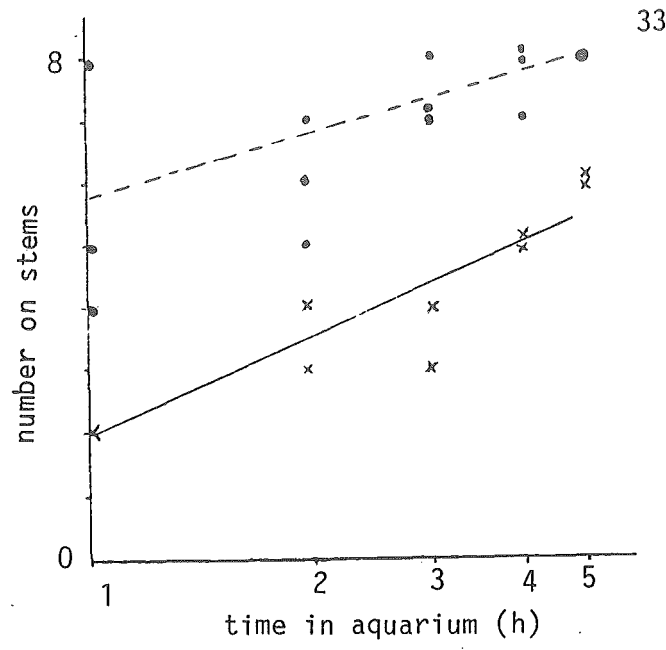


Fig. 37. Stem diameter preference in final-instar X. zealandica larvae.

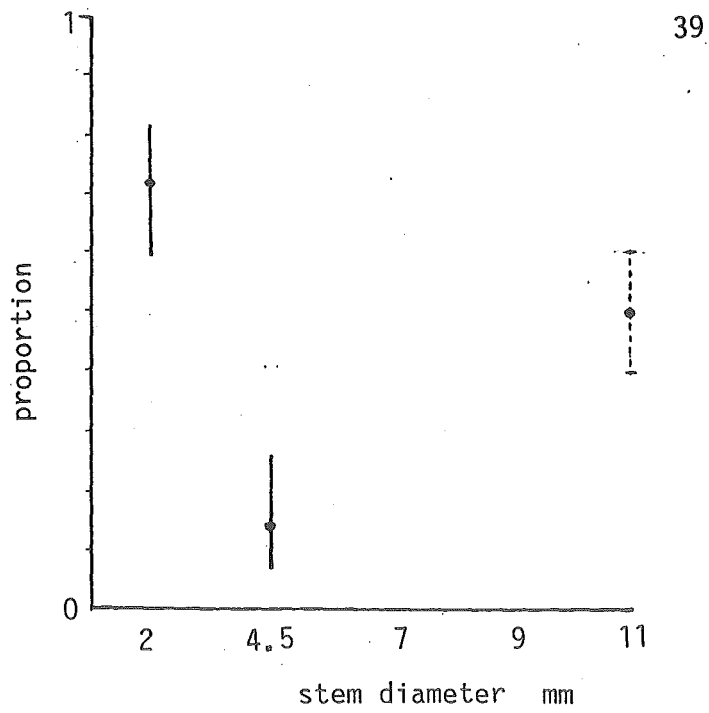
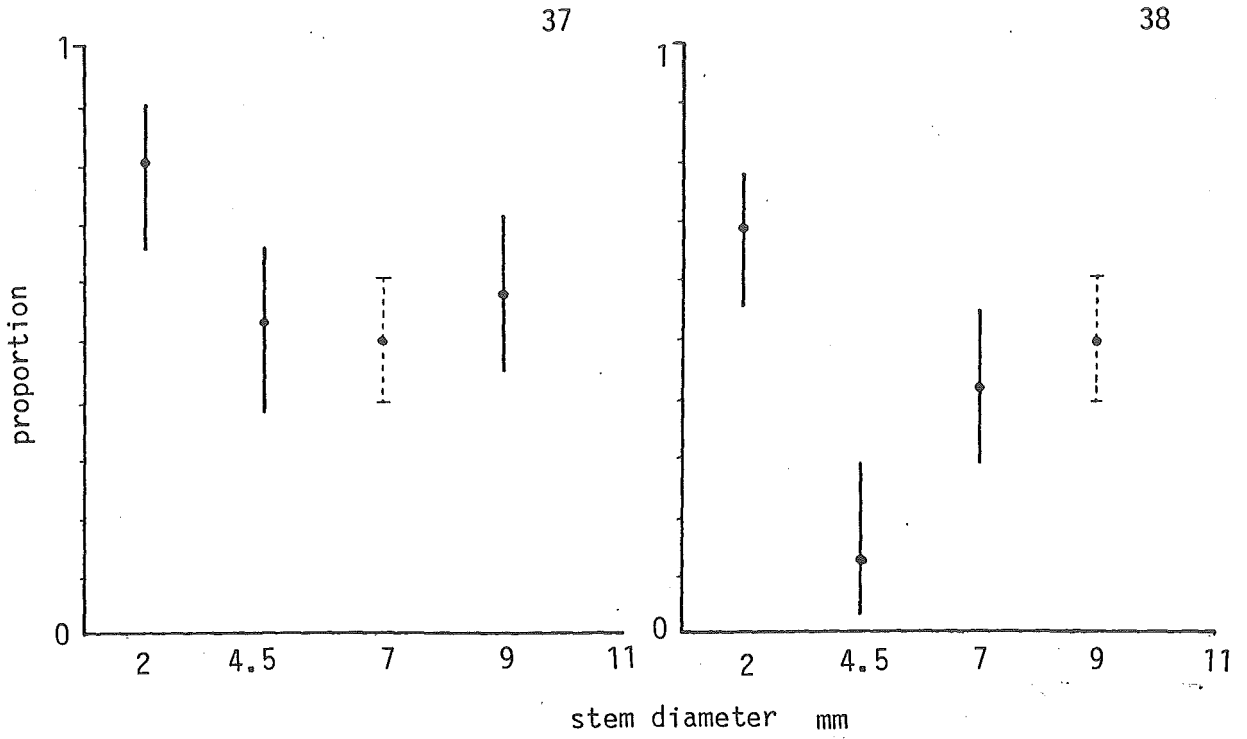
Eight larvae were held for 48h in an aquarium with 8 x 7mm diameter stems and 8 stems of another diameter. The graph shows the proportion of larvae on stems that occupied the 7mm diameter stems (see text). The 95% confidence intervals are indicated.

Fig. 38. Stem diameter preference in final-instar X. zealandica larvae.

Eight larvae were held for 48h in an aquarium with 8 x 9mm diameter stems and 8 stems of another diameter. The graph shows the proportion of larvae on stems that occupied the 9mm diameter stems (see text). The 95% confidence intervals are indicated.

Fig. 39. Stem diameter preference in final-instar X. zealandica larvae.

Eight larvae were held for 48h in an aquarium with 8 x 11mm diameter stems and 8 stems of another diameter. The graph shows the proportion of larvae on stems that occupied the 11mm diameter stems (see text). The 95% confidence intervals are indicated.



Figs 40-43. Stem diameter preference by smaller larvae (headwidth 1.2-1.8 mm).

Fig. 40. Proportion of larvae on the alternative to 2 mm stems after 48h.
(larvae from L. Grasmere, Cass, 29 Jan. 1981)

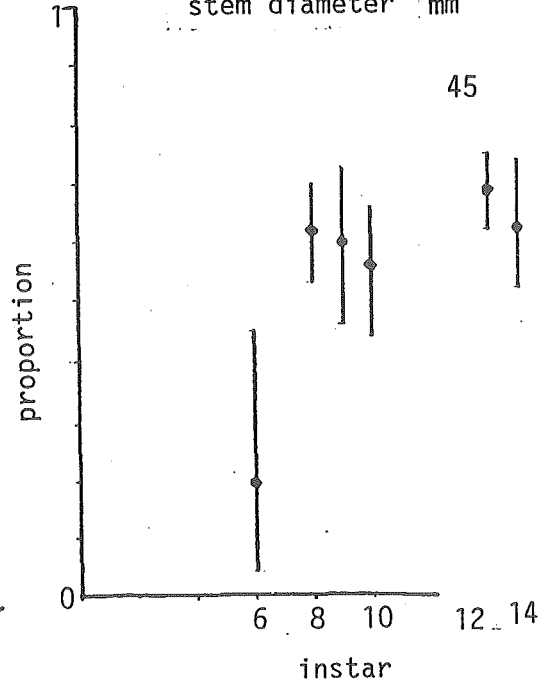
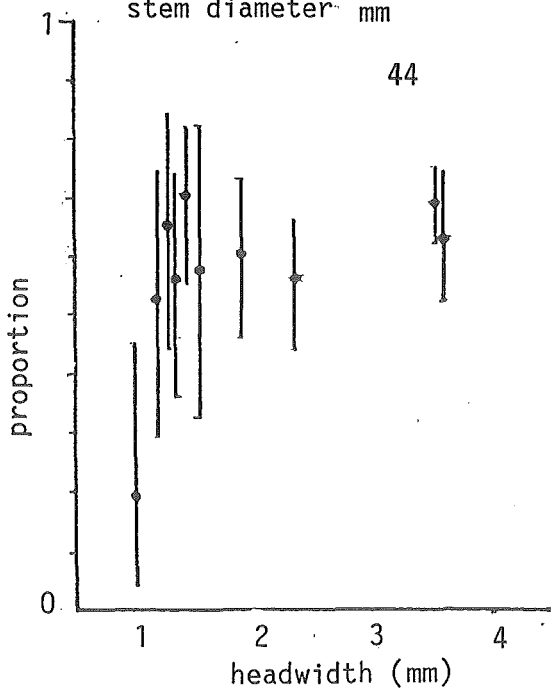
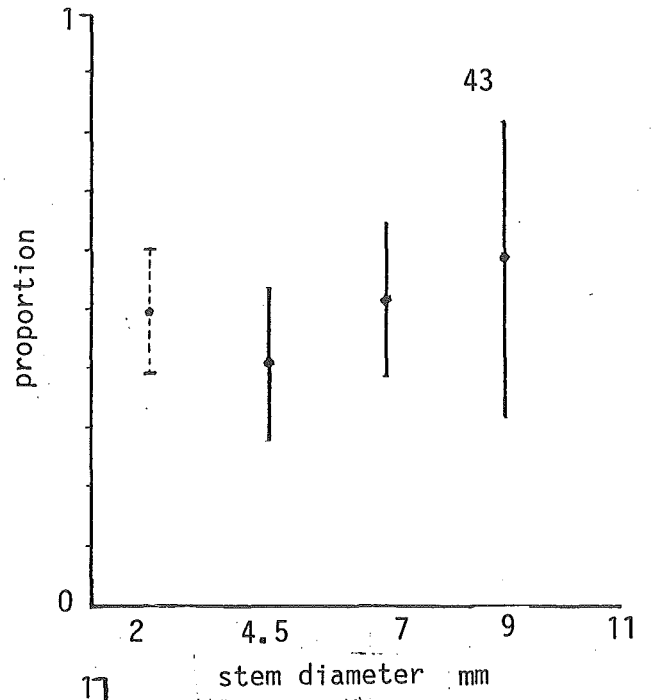
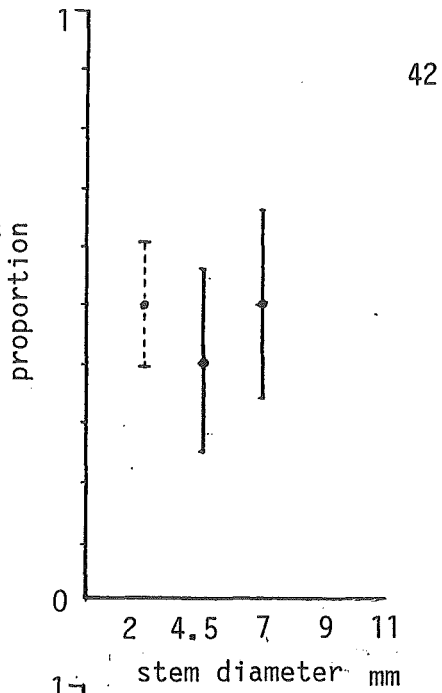
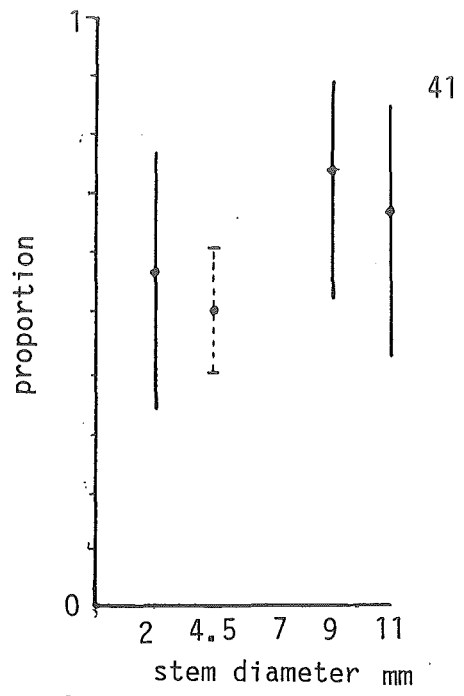
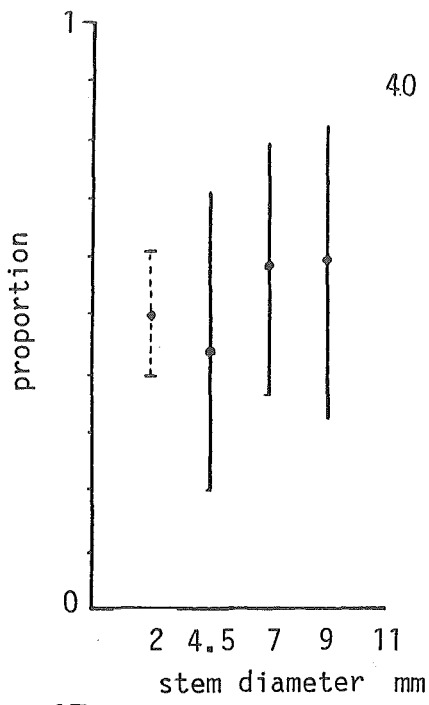
Fig. 41. Proportion of larvae on 4.5 mm stems after 48h.
(larvae from L. Grasmere, Cass, 29 Jan. 1981)

Fig. 42. Proportion of larvae on the alternative to 2 mm stems after 48h.
(larvae from Belfast, Christchurch, 11, 23 Feb. 1981)

Fig. 43. Cumulative proportion of larvae on the alternative to 2 mm stems after 48h (data in Figs 40 and 42 combined).

Fig. 44. Proportion of larvae of a range of sizes on the alternative to 2 mm stems after 48h (headwidth v preference).

Fig. 45. Proportion of larvae of a range of sizes on the alternative to 2 mm stems after 48h (putative instar v preference).



Site utilisation experiments

Diel activity patterns. Activity levels of larvae during the light and dark periods were significantly different (Mann-Whitney U-test, $U = 34.5$, $n_1 = n_2 = 6$, $P < 0.05$). However, the total amount of activity recorded was very low. During the light phase, individual larvae averaged fewer than 0.25 movements h^{-1} while in the dark the same larvae each averaged fewer than 0.4 movements h^{-1} .

Moulting. A total of 56 moults occurred during the course of the investigation. Of these, 34 occurred on 4.5-mm diameter stems under conditions where detailed analysis of the sequence of immediate pre- and post-moulting behaviour was justified; the remainder involved some (later) interference. Moulting was observed on several occasions and always took less than 5 minutes to complete. Time of moulting in relation to total duration of occupation is presented as a scattergram (Fig. 46). Half (17 of 34) the moulting larvae abandoned their perches within a day of ecdysis. The presence of exuviae below the original perch was evidence that moulting had been completed prior to movement occurring. Most of the larvae which abandoned perches had been on the stem only a few days at the time of moulting. The duration of occupation at the time of the moult is presented as a semi-log cumulative frequency graph (Fig. 47). Some 'structure' appears to be present, but the data set is not large enough to determine what it is. Most moulting occurred either shortly after the commencement of occupation, or after a long time on the site. Site occupation after moulting, for those larvae which remained on the site, approximated to a negative exponential distribution with a slow rate of decay (Fig. 48). Larvae unmoved by the immediate stresses of moulting did not have their stem occupancy behaviour altered.

Location and body orientation of larvae on the two days prior to, the day of, and the two days following a moult (Table 21) were

Fig. 46. Time of moulting v duration of total occupation of site. All larvae on the dashed 'y = x' line abandoned the stem after moulting.

Fig. 47. Semi-log cumulative graph of the duration of occupation at the time of moulting.

Fig. 48. Semi-log cumulative graph of the duration of occupation after the time of moulting.

$$\ln(\text{cumulative frequency}) = 2.63 - 0.094 \times \text{duration}; r = -0.976$$

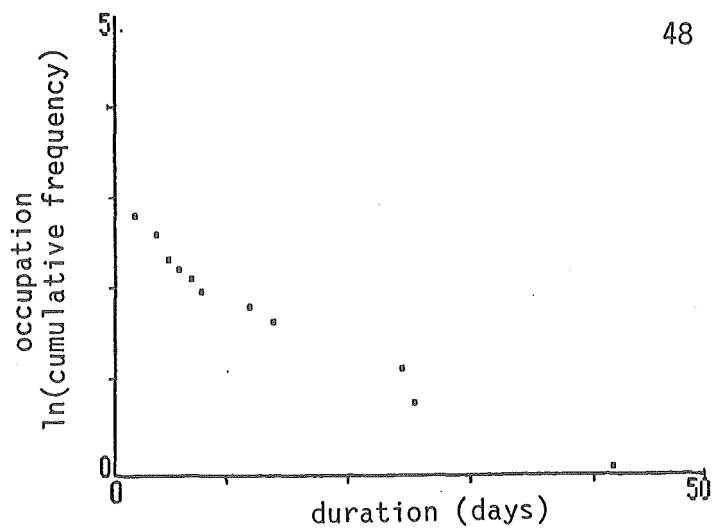
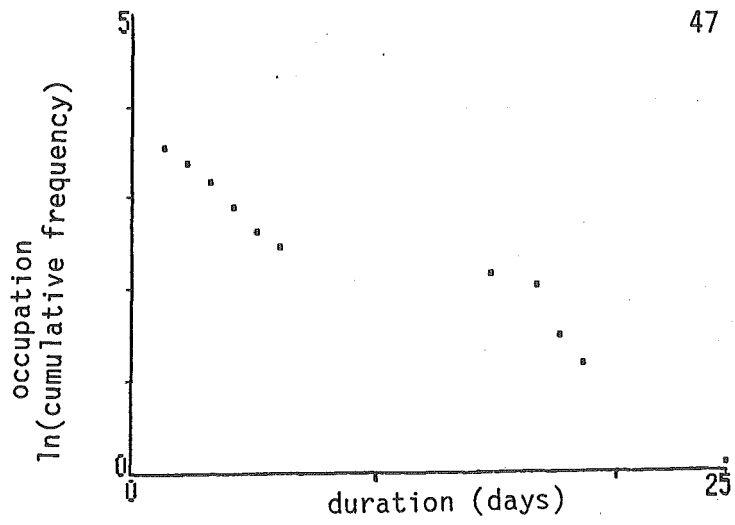
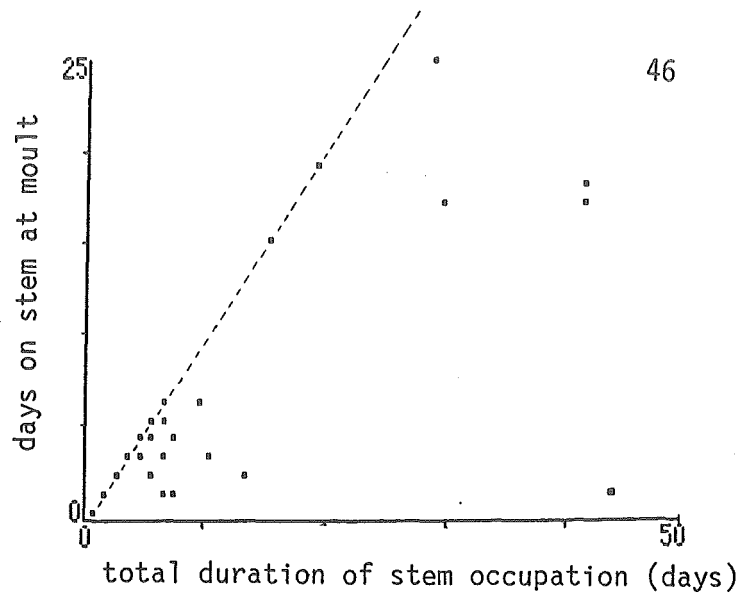


Table 21. Larval location and orientation on stems at moult.

Larval site behaviour on the two days prior to moulting, the day of moulting and first two days after moulting were abstracted. For each of the height intervals distinguished during this investigation the numbers of larvae facing up or down are shown.

height intervals (cm)	0-3		3-6		6-9		9-12	
orientation:	down	up	down	up	down	up	down	up
For the two days prior to moulting	26	2	9	4	3	6	8	2
On the day of moult	17	4	2	2	7	4	7	3
For the two days after moulting	31	18	5	8	5	3	2	4

compared. On the day following a moult 82% of larvae were on perches. By comparison, long term perch occupancy of all larvae over all aquaria was 84%, (S.D. 13.5%, $n = 41$). Thus, while larvae frequently abandoned their perches on moulting they quickly took up residence on another site.

To establish if changes in site usage accompanied moulting Chi-square comparisons were done testing for differences in height and orientation before and after moulting. Use of the bottom level, the preferred location of undisturbed larvae, was compared with the other levels (combined) for the two days prior to and the two days after moulting. While larvae had a propensity to be higher on their stems before moulting this trend was not statistically significant ($\chi^2 = 3.63$ $p < 0.1$).

Orientation before and after moulting was compared also for larvae on the bottom level and for all other levels combined. Prior to moulting larvae at the bottom of stems almost invariably faced downwards (26 of 28 larva-days) whereas at higher levels (20 of 32 larva-days) and immediately after moulting (31 of 49 larva-days) this pattern breaks down. The change in behaviour pattern of larvae at the bottom of stems was highly significant ($\chi^2 = 6.64$ $p < 0.01$).

Emergence. During the study, 28 X. zealandica larvae underwent metamorphosis and emerged under conditions considered suitable for analysis. Site occupation and orientation during the 10 days prior to emergence and on the last day of aquatic life are shown in Table 22. Only at the lowest stem level were occupation frequencies appropriate (Conover 1980) to test for changes in orientation ($X^2 = 2.25$, ns). No significant differences in the numbers of larvae occupying different stem heights during the ten days prior to emergence and on the last day of aquatic life were discerned using the Anderson-Darling Cramer von Mises statistic (heuristic in Conover 1980) ($z = 0.11$, $0.54 > P > 0.53$, ns).

Some larvae, however, did move to the top of stems and faced the surface of the water for several days before emerging. This was not a common behaviour.

On one occasion, an emergence was observed in full. The larva was at the base of its stem facing up. Suddenly it walked to the top of the stem, paused for about 2 minutes at the surface and then climbed out of the water. Within 5 minutes of beginning its climb it had settled on a site on the stem support framework and begun the process of emergence which took 40 minutes.

Table 22. Larval position and orientation on perches during the 10 days prior to emergence and on the day of emergence.

height intervals (cm)	0-3		3-6		6-9		9-12		12-		br*	ro*
orientation:	down up		down up		down up		down up		down up			
10 days prior	7	3	1	0	2	1	1	5	1	1	0	3
emergence day	3	8	5	4	1	1	2	0	1	1	1	1

* br = on branches, ro = on roots.

Occupation of stems and other sites

The positions occupied by larvae alone on stems are tabulated in Appendix 4. Except when Lumbriculus prey were offered and 2-mm diameter stems were provided food type appeared to have no significant influence on site choice. Site occupation by X. zealandica in the absence of prey and with Opifex as prey is analysed below. Because of the apparent indifference to prey type, passing comments only are made below for the other prey types used.

Positions occupied on stems. In the standard 8 larvae - 8 stem aquarium larvae tended to be at the bottom of the stem under all experimental conditions (Figs 49-53), and almost all larvae were on perches throughout the observation period (Figs 54-58).

Stems v other sites. On 11 occasions, aquaria were operated with 8 stems (or trees), each with a below water length of about 10 cm, and three 10 cm long 'roots' of 4.5-mm tube. Observation time totalled 287 days and provided about 2000 larva-day records. The mean proportion of root occupancy was 23.5% (S.D. = 11.0%, n = 11) an insignificant difference from the 27.3% of sites provided by roots. It would appear that a stem, tree or root of this length represents a single site available for occupation.

'Branches' or 'leaves'. Occupation of bare 2-mm diameter branches or polyethylene 'leaves' was contrasted in four aquaria with Simocephalus, and one aquarium with Daphnia prey. For logistic reasons (the prey cultures died out) these experiments were short term and this may account for the relatively high rate of branch/'leaf' occupation in comparison to that found in the long run experiments. Crowley (1979) commented that Simocephalus tend to occur on surfaces; this was borne out by my observations of prey behaviour.

Figs 49–53. Representative examples of larval position and orientation on stems. Solid bars indicate the proportion of larvae at the given level. Hollow bars indicate the proportion of larvae at that level facing up towards the surface.

Sites examined at noon daily. Only data from animals alone on a stem presented. Complete data set in Appendix 4.

Fig. 49. Larvae on 4.5 mm diameter stems with no food, $n = 89$.

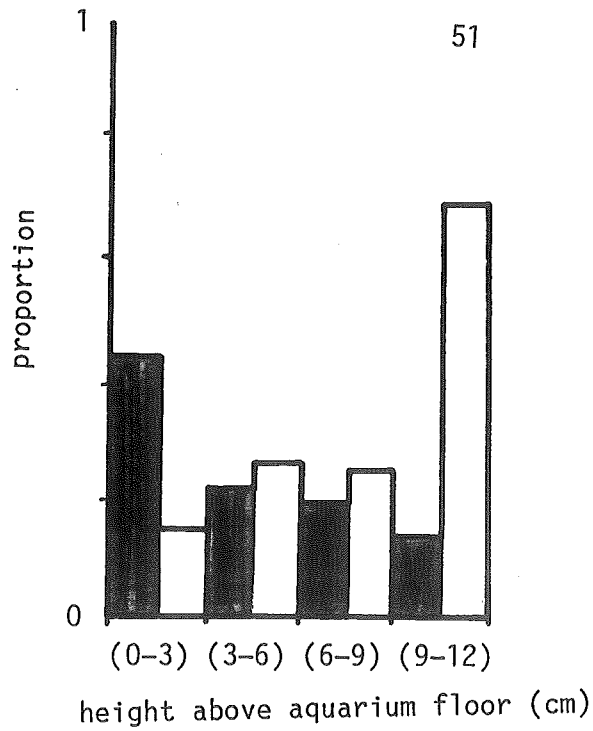
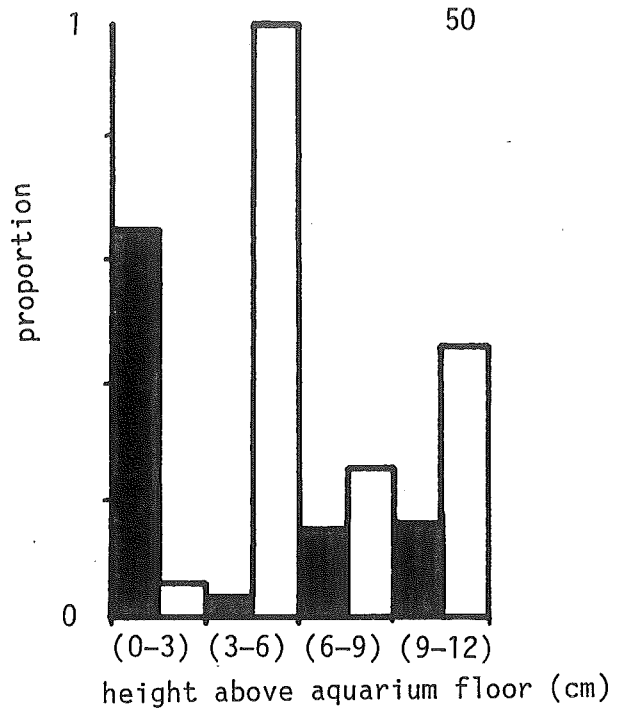
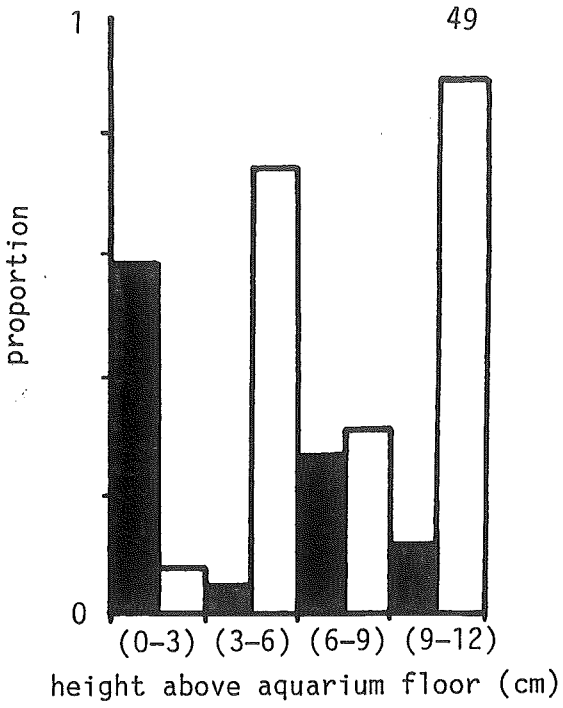
Fig. 50. Larvae on 2 mm diameter stems with no food, $n = 81$

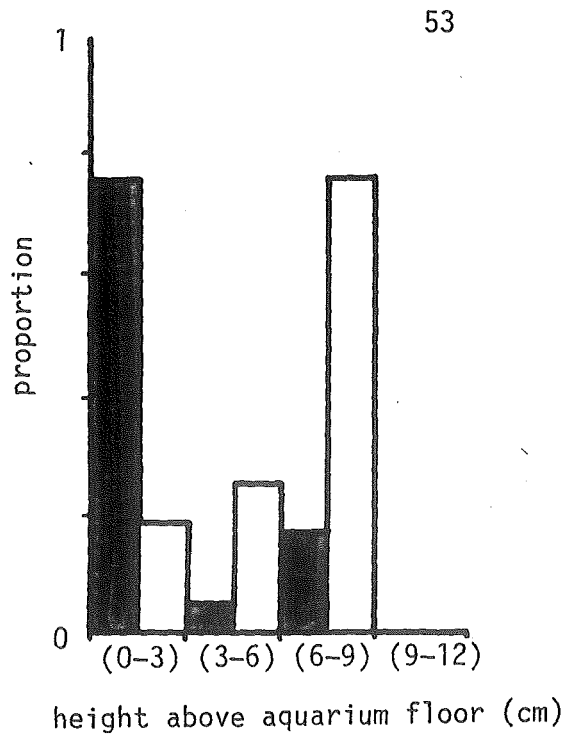
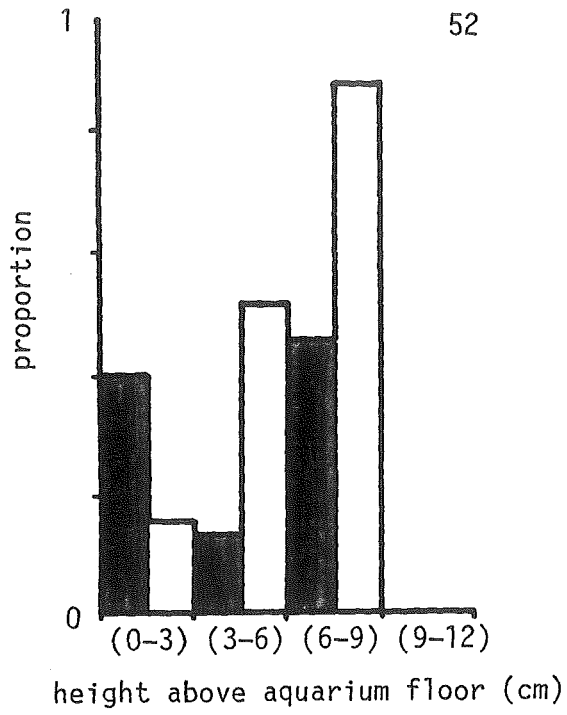
Fig. 51. Larvae on 4.5 mm diameter stems with Simocephalus as food, $n = 122$

Fig. 52. Larvae on 4.5 mm diameter stems with Simocephalus as food, $n = 144$

Fig. 53. Larvae on 7 mm diameter stems with Simocephalus as food, $n = 77$

Data shown in Figs 52 and 53 were obtained simultaneously in the same aquarium.





Figs 54–58. The proportion of larvae occupying stems is graphed as a function of time, using a series of scales of measurement. No periodicities or long term changes in the proportion of stem usage were observed.

Fig. 54. Aquarium examined daily at noon and approximately at 2h intervals through the night for 5 days. Food = Simocephalus

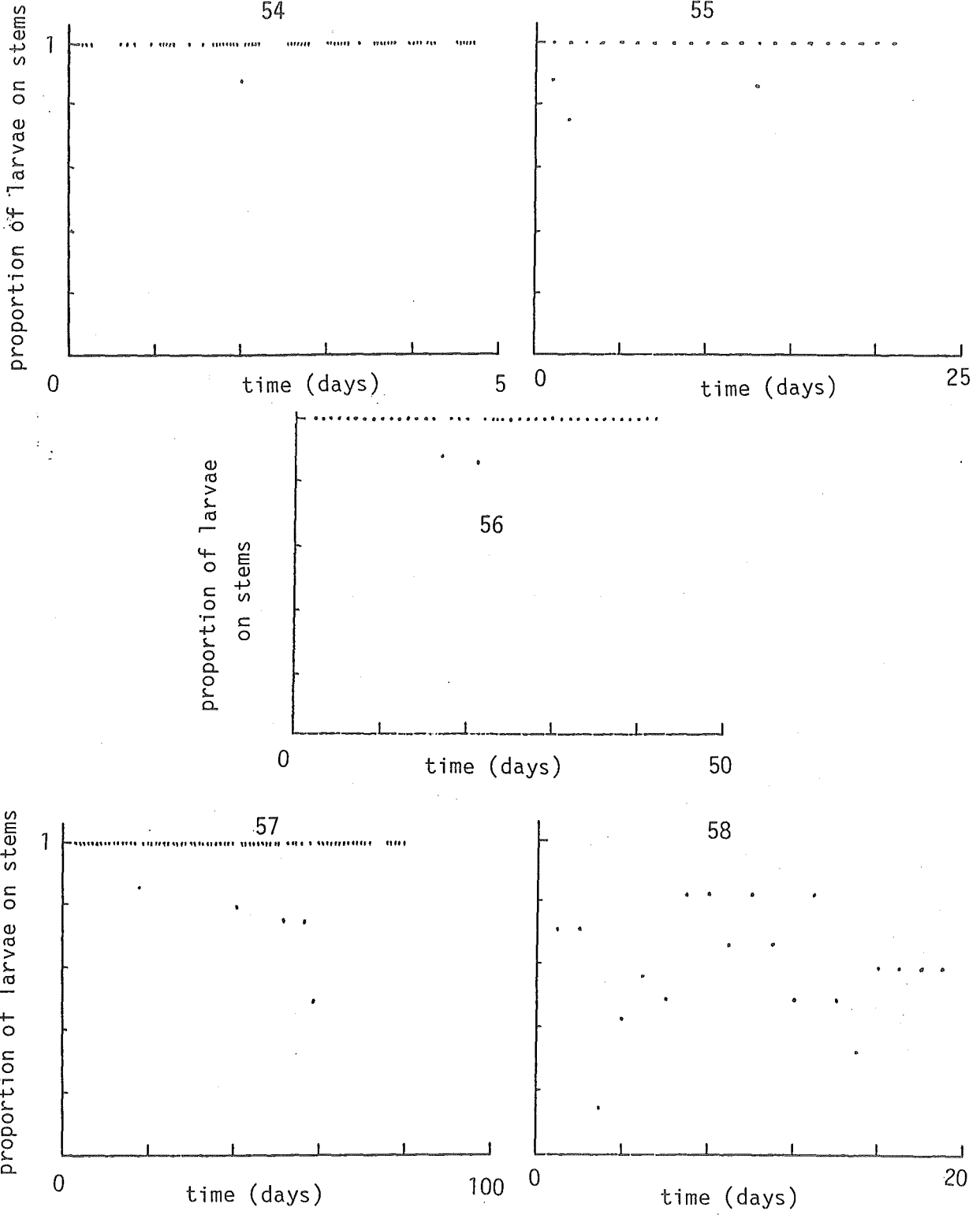
Fig. 55. Aquarium examined at noon and 3PM for 22 days.

Food = Simocephalus

Fig. 56. Aquarium examined at noon for 45 days. Food = Simocephalus

Fig. 57. Aquarium examined at noon for 80 days. Food = Simocephalus

Fig. 58. The only exceptions to the sedentary behaviour pattern occurred when larvae on 2-mm diameter stems were fed Lumbriculus.



With Daphnia as prey, larvae spent 36% of their on-stem time on leaves and 38% on bare branches (39 and 45 larva-days respectively). With Simocephalus, 42% of the on-stem time was on leaves and 55% on bare branches. Given the variation found, these results could not be regarded as different. A comparison of branch vs leaf occupation for the Simocephalus experiments indicated an insignificant difference (one way ANOVA on the $\arcsin(\sqrt{x})$ transformed frequency values $F_{[1,6]} = 3.962$, $P < 0.1$).

Effects of 'branch' diameter. Two different types of 'tree' were used, one with 4.5-mm diameter branches inserted in 7-mm diameter stems, and the other with 2-mm diameter branches in 4.5-mm diameter stems. 'Branches' were all about 3 cm long. Larvae feeding on Simocephalus and Daphnia were offered 8 'trees', 4 of each type. With Simocephalus fed larvae, 4 of 148 occupations of 4.5-mm diameter stemmed trees were on the 2-mm diameter branches whereas 18 of 85 occupations of 7-mm diameter stemmed trees were on the 4.5-mm diameter branches. Daphnia fed larvae spent 1 of 57 occupations of 4.5-mm diameter stemmed trees on the 2-mm diameter branches and 21 of 57 occupations of 7-mm diameter trees on the 4.5-mm diameter branches. Thus with 4.5-mm diameter trees and 2-mm branches about 2-3% of the site occupancy was on branches, the rest of the larvae using the stem of the 'tree'. When offered 4.5-mm branches about 20-37% of site occupancy was on branches. Heavier occupancy of 4.5-mm diameter stems (148) compared with 7-mm diameter stems (85) in the aquarium with Simocephalus prey was probably a consequence of the lack of independence of sequential observations; similar discrepancies in counts occurred occasionally between rows of physically similar stems. While 2-mm diameter branches were not favoured, 4.5-mm diameter branches were used commonly.

Use of 2-mm branches with various prey species present. The use of 2-mm branches was abstracted for all four prey types used, and compared. While mean branch usage with Daphnia (which occurred in midwater) was somewhat higher than for other prey there was no significant deviation in usage among the prey types (ANOVA, data arcsin(SQR(x) transformed, $F_{[3,20]} = 1.176$ $P < 0.344$).

Temporal patterns

The temporal pattern of site usage did not vary with the different prey types used. However, the duration of site occupancy varied markedly with site geometry (Figs 59-63). In general, duration of occupation data were well approximated by a negative exponential distribution (r values of the semi-log regression typically > 0.95). The 'halflife' of site occupation was about 1.2 days for 2-mm stems; about 2.4-4.2 days for 4.5 mm stems; about 1.5 days for 4.5-mm diameter roots and about 3.5 days for 7-mm diameter stems.

Use of artificial plants

Because larvae are cryptic and hard to detect, it was only practical to place a few animals with artificial plants at one time. Because of lack of independence, the data were not amenable to statistical analysis.

On facsimile Potamogeton, larvae localised on individual leaves and mean residence time on a leaf was 1.5 days (S.D. = 1.1, $n = 57$); mean residence time on a 'plant' was 1.9 days (S.D. = 1.8, $n = 44$). Most observed movements occurred on the occupied leaf and involved either a change of direction or a movement around the leaf. Of movements on a plant most (9 of 13) involved movement to an adjacent leaf. Larvae rarely occurred on adjacent leaves.

The facsimile charophytes were trident shaped and consisted of a short basal stem, a cross piece and three fronds. The basal stem and each

Fig. 59. Semi-log cumulative graph showing the duration of occupation on 4.5-mm diameter stems. Least squares fitted line:

$$\ln(\text{cumulative frequency}) = 3.26 - 0.095 \times \text{duration}; r = -0.981$$

Fig. 60. Semi-log cumulative graph showing the duration of occupation on 7-mm diameter stems. Least squares fitted line:

$$\ln(\text{cumulative frequency}) = 3.65 - 0.209 \times \text{duration}; r = -0.975$$

Fig. 61. Semi-log cumulative graph showing the duration of occupation on 4.5-mm diameter roots. Least squares fitted line:

$$\ln(\text{cumulative frequency}) = 4.24 - 0.463 \times \text{duration}; r = -0.982$$

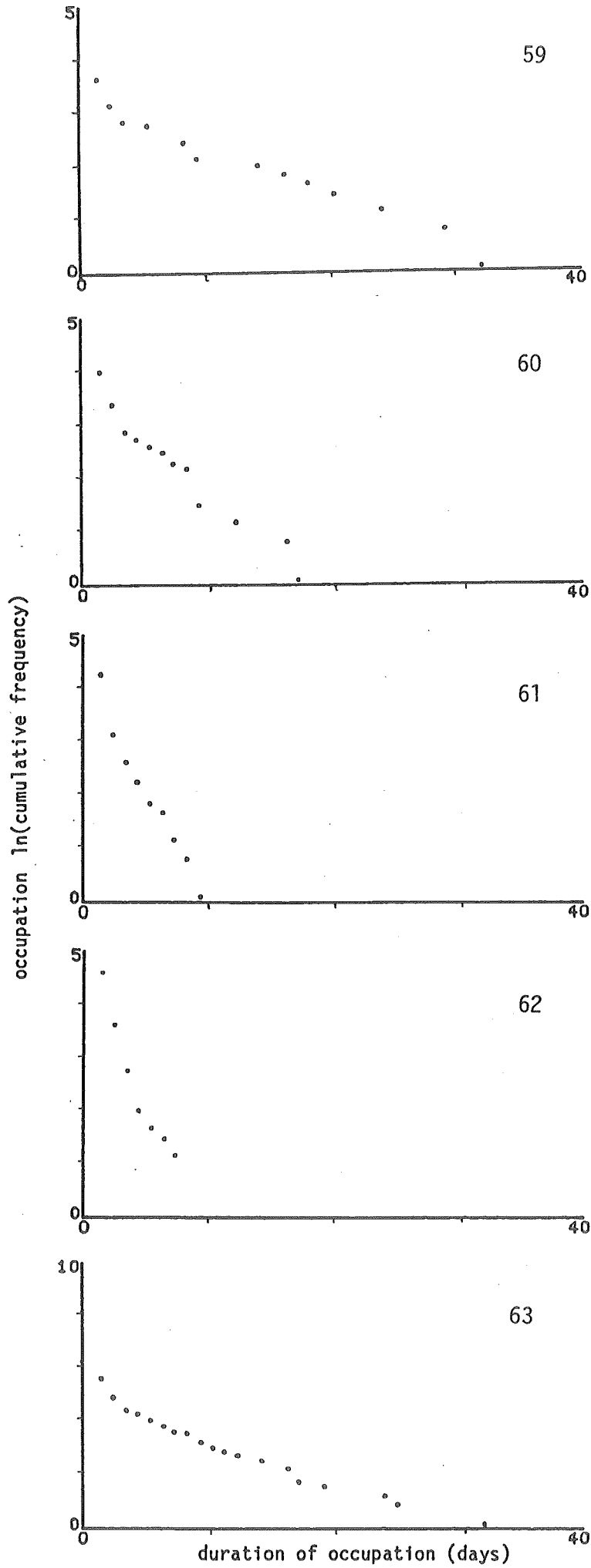
Data shown in Figs 59 - 61 were obtained simultaneously in the same aquarium.

Fig. 62. Semi-log cumulative graph showing the duration of occupation on 2-mm diameter stems. Least squares fitted line:

$$\ln(\text{cumulative frequency}) = 4.68 - 0.567 \times \text{duration}; r = -0.962$$

Fig. 63. Semi-log cumulative graph showing the duration of occupation on 4.5-mm diameter stems. Least squares fitted line:

$$\ln(\text{cumulative frequency}) = 4.80 - 0.166 \times \text{duration}; r = -0.975$$



of the fronds appeared to represent separate sites. Larvae localised, and remained for many days, on such sites. Mean duration of occupation on a frond was 1.9 days (S.D. = 1.9, $n = 56$) and mean duration on a 'plant' was 4.0 days (S.D. = 4.6, $n = 26$) (Fig 64). Larvae occupying fronds tended to be found facing downwards near the basal junction with the cross piece. Occasionally, they roved about the frond for some hours before resettling at the base. Two larvae rarely occurred together on a site, but on occasions when they did territorial displays and expulsion of invaders was observed.

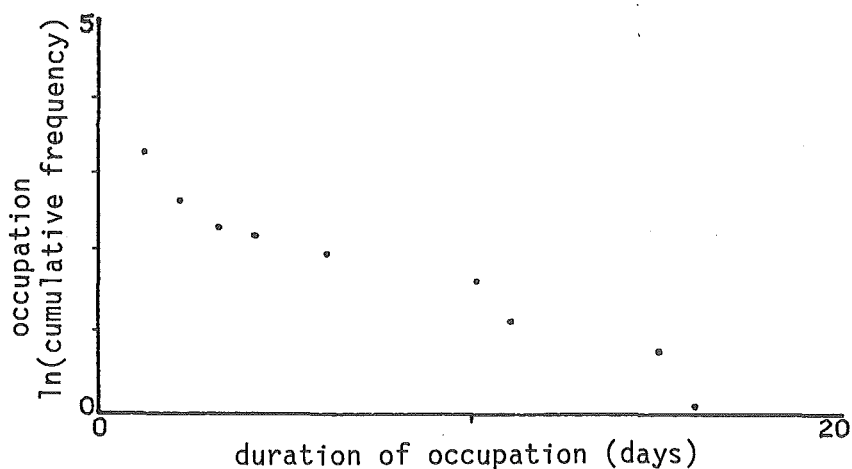


Fig. 64. Durations of occupation on 'charophytes'.

$$\ln(\text{cumulative frequency}) = 3.0 - 0.175 \times \text{duration}; r = -0.97$$

Site usage in the absence of prey

Site usage in the absence of prey was examined in three standard aquarium 'set ups'. Larvae were assigned randomly to aquaria, marked and released. Site occupation and usage by larvae was monitored for at least two weeks prior to the removal of food. The larvae were then transferred to aquaria without food and site occupation and usage was recorded.

Behaviour in the period without food was contrasted with both the behaviour prior to the removal of food and the behaviour of larvae in a 'control' aquarium which had the same treatments, but with food present.

In the first experiment, larvae were maintained on 2-mm diameter stems with L. variegatus as prey. They were then shifted with their stems to an aquarium without food. In the second experiment, larvae were maintained on 4.5-mm diameter stems with Simocephalus as prey and were shifted on their stems to an aquarium without food. In the third experiment, larvae were maintained on 2-mm diameter stems with Simocephalus as prey and were shifted to 4.5-mm diameter stems in an aquarium without food. After 15 days (experiments one and two), or 21 days (experiment three) without food, Lumbriculus was added to the experimental aquaria and behaviour of larvae was noted.

Larval usage of stems through the experimental period under each regime is shown in Table 23. Orientations of fed and starved larvae were compared for each height interval using 2 x 2 contingency tables. Because of the lack of independence between observations this test will be non-conservative; nonetheless, no 'significant' differences in orientation were found. With orientations pooled, the distributions of larvae along stems were compared pairwise for all experiments using the Anderson-Darling Cramer von Mises statistic (Conover 1980). Again, lack of independence would tend to promote a non-conservative result and again no 'significant' differences were found in the height of larvae above the substrate.

The proportion of larvae on stems differed between treatments (Table 23). However, the marked divergence of results obtained in experiment one from the pattern obtained under the other regimes was due to the anomalous behaviour of a single larva which did not occupy a stem. Larvae offered 2-mm stems and fed L. variegatus had a low rate of stem occupancy. However, when on stems, they occupied the same positions as larvae under other regimes. There was no difference in the durations of site occupation between larvae with and without food (Figs 65, 66).

Table 23. Stem usage by larvae before (a) and during (b) a prolonged period of starvation.

Conditions:

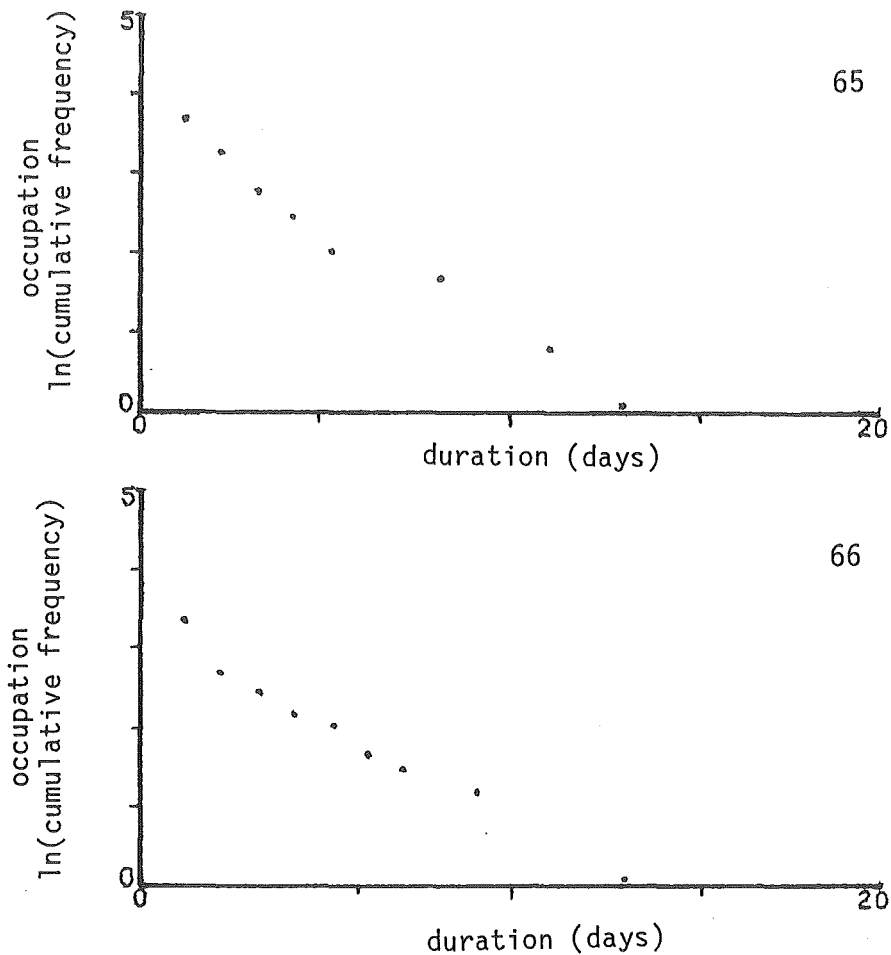
- Experiment 1 a) 2-mm diameter stems, L. variegatus prey
b) 2-mm diameter stems, starved 15 days
- Experiment 2 a) 4.5-mm diameter stems, S. exspinosus prey
b) 4.5-mm diameter stems, starved 15 days
- Experiment 3 a) 2-mm diameter stems, S. exspinosus prey
b) 4.5-mm diameter stems, starved 21 days

Larval positions (height on stem, facing up or down) recorded daily at noon. 'On stems' records the number of stem occupations and the maximum possible number of occupations during the observation period. The percentage occupation of stems is given.

height intervals (cm)		0-3		3-6		6-9		9-12		'on stems'	%
orientation		down	up	down	up	down	up	down	up		
experiment 1	a	22	2	7	1	24	14	5	17	118/224	53
	b	50	3	0	3	9	3	7	6	98/131	75
experiment 2	a	57	8	5	1	7	6	2	36	174/228	76
	b	48	4	1	3	16	7	1	9	112/124	90
experiment 3	a	85	4	10	10	10	6	3	24	187/196	95
	b	57	1	4	1	14	14	1	16	205/208	99

Site usage with Opifex fuscus larvae as prey:

Larvae of Opifex fuscus are similar to those of Culex pervigilans (Bergroth) which is known to be preyed upon heavily by X. zealandica larvae at Cass pond, the source of damselfly larvae used in my experiments, during brief seasonal periods of abundance (Dowdle 1981). O. fuscus spent most of their time 'drifting' near the bottom of aquaria and feeding from the floor. If alarmed, and on some other occasions, they swam horizontally across an aquarium using wriggling movements. Every few minutes they would swim to the surface and hang



Figs 65, 66. Semi-log cumulative graphs showing the duration of site occupation by eight larvae maintained on the same 4.5 mm diameter stems prior to and during a prolonged period of starvation.

Fig. 65. Fed *Simocephalus*. Least squares fitted line:

$$\ln(\text{cumulative frequency}) = 3.67 - 0.28 \times \text{duration}; r = -0.988$$

Fig. 66. Starved for 15 days. Least squares fitted line:

$$\ln(\text{cumulative frequency}) = 3.32 - 0.26 \times \text{duration}; r = -0.991$$

there for some time taking in air, before sinking slowly down to resume feeding. Most observed attacks on *O. fuscus* larvae were directed at feeding animals as they moved slowly across the floor of the aquarium past an *X. zealandica* perch. The positions and orientations of larvae when fed *Opifex* are shown in Table 24. There were no significant departures from the pattern of site usage found with other prey.

Table 24. Site usage of X. zealandica larvae fed O. fuscus.

Larvae were offered one of: 8x 2-mm diameter stems, 8x 4.5-mm diameter stems, 8x 4.5-mm diameter trees with 2-mm diameter branches, 4x 2-mm diameter stems + 4x 4.5-mm diameter stems. In addition some aquaria had 3x 4.5-mm roots.

height intervals (cm)	0-3		3-6		6-9		9-12		ro*		br*	
orientation:	down	up	down	up	down	up	down	up	in	out	in	out
sites present												
4.5-mm stems-3 roots	119	14	27	17	16	9	0	0	29	55		
4.5-mm stems-3 roots	221	5	11	6	4	3	0	0	3	2		
8 trees	84	11	33	15	7	8	0	0			3	1
8 trees-3 roots	16	1	11	2	2	0			2	9		
4.5-mm+2-mm stems	34	10	14	6	0	3						[4.5mm]*
	34	3	4	4	2	2						[2mm]*
4.5-mm+2-mm stems	22	7	3	1	0	2						[4.5mm]*
	10	2	5	5	1	2						[2mm]*

* ro = roots, br = branches, [4.5mm] denotes animals on 4.5-mm stems, [2mm] denotes animals on 2-mm diameter stems

Site usage with Lumbriculus, Simocephalus and Daphnia prey.

Lumbriculus, Simocephalus and Daphnia represented prey with markedly different behaviour patterns. In the aquaria used in this investigation, almost all Lumbriculus remained on the floor of the aquarium; Simocephalus swam over the bottom of the aquarium and moved along the surfaces of roots, stems, branches and leaves; Daphnia swam actively in midwater, often forming large aggregations. Except when larvae were on 2-mm stems and were fed Lumbriculus, there was no marked departure from the pattern of site usage found with other prey. Larvae offered 2-mm diameter stems and Lumbriculus spent much of their time off stems. If this represented a 'searching' behaviour, then its absence when larger diameter stems were present and when no prey were present is problematical.

Density

In two of four aquaria containing a solitary larva and 8 stems, the larva made several short duration (1-2 day) occupations before settling for the duration of the investigation. In the other two aquaria the larvae took up residence immediately, and remained at a single site for the duration of the investigation. All larvae had occupied their sites for more than 10 days at the termination of the experiment.

Investigations of larval behaviour at high densities were largely frustrated by high mortality (with 1-2 animals dying each day). The experiments had to be abandoned as the densities could not be controlled adequately. Larvae tended to move about more than they had at lower densities, nevertheless some individuals established themselves on particular perches for many days and displayed territorial behaviour.

Intraspecific interactions

Despite a very large number of site occupations being recorded, there were too few repeated interactions between larvae to analyse for the occurrence of any sort of hierarchy. Interactions where the invader failed to establish itself on the perch almost invariably involved a conflict lasting less than a day. Observations made while investigating agonistic displays (Chapter 2) indicated that such conflicts often lasted only a few seconds to 5 min - a timescale far too short to be analysed here. However, a number of long conflicts, lasting up to 15 days, were observed. In all such situations the invading larva occupied the bottom of the stem and the original resident was either 'head up' (see Chapter 2) if the original resident was markedly smaller than the invader, or perched 2-5 cm above the invader and facing down.

When the distributions of larvae on stems with a single occupant were contrasted with distributions on multiply occupied stems, no statistically significant differences were found (data tabulated in Appendix 4).

Two fortuitous observations were made of conflicts where occupants were forced off their stems and, after walking a few centimetres from the stem, paused, turned about, walked back to the stem and climbed back on. In both instances the original resident was the sole occupant the following day.

Austrolestes colenisonis

When offered 4.5-mm stems, A. colenisonis larvae occupied them on only 8 of 40, 3 of 24 and 14 of 75 larva-days, an overall occupation rate of 18%. When offered 11-mm diameter stems the A. colenisonis larvae were on them on 35 of 91 possible occasions, an overall occupancy rate of 38.5%. Both of these occupancy rates were far below those found with X. zealandica. On only one occasion was an A. colenisonis larva recorded on the same stem on successive days and this may have been a chance recolonisation of the same stem. Observations at night showed a higher proportion of stem usage than during the day (sometimes 6 or more of the 8 larvae in an aquarium were hanging from stems). During the day and at 'night', larvae of this species were very easily disturbed while on stems and the investigation was not pursued further. A. colenisonis larvae are often seen walking about on the bottoms of shallow ponds during the day and the failure to occupy stems did not appear to be a response to stressful laboratory conditions.

DISCUSSION

The responses of larvae offered a choice of stems appeared to vary somewhat between samples (Fig. 34). However, given the difficulties inherent in statistics of proportion this was not unexpected. These difficulties were also reflected in the range of confidence intervals obtained. Final instar larvae appeared to prefer stems of any diameter to the 'infinite' diameter presented by the aquarium wall and of the stem

sizes offered (2-, 4.5-, 7-, 9- and 11-mm diameter) the 2-mm stem was consistently the least favoured. However, the data indicate that larger diameter stems were not as attractive as the 4.5 - 7-mm diameter stems. When 4.5- or 7-mm diameter stems were offered a distinct preference for them was apparent. The data were not extensive enough to indicate a statistically significant difference in preference between these two diameters but the absence of strong discrimination between them would seem to imply that there is no biological significance in the choice. When 9-mm stems were offered as the alternative to 4.5-mm stems a distinct preference for the latter was apparent. Because of experimental difficulties, few choice comparisons could be made with 11-mm diameter stems as the alternative to 4.5-mm stems. A lack of consistency in stem preference between larvae collected in summer and autumn may have been a seasonal effect. Larvae collected in autumn would have moulted into the final instar recently and would be about to overwinter (Deacon 1979, own unpubl. obs.). A number of coenagrionid larvae appear to move to different habitats prior to overwintering (Macan 1964, 1977, Lawton 1970a, Johannsson 1978) and such a change would be consistent with the known difficulties in obtaining X. zealandica larvae during winter (Rowe 1978a).

Kime (1974) examined the effect of perch diameter on site selection in two aeshnid (Anisoptera) species. In choice experiments she found that the active larvae of Anax junius Drury, which stalked and pursued prey, used even the smallest diameter sites offered, whereas later instars of the 'sit and wait', ambush predator Aeshna californica Calvert had a marked preference for larger perch diameters (Table 25). Kime also noted that smaller A. californica larvae colonised stems indiscriminately so long as the diameter was greater than 6 mm. In X. zealandica, also a 'sit and wait', ambush predator, the effect of site diameter was more

Table 25. Perch selection by final instar aeshnid larvae in a large water table (presumably a large, shallow aquarium) (Table XVII of Kime 1974).

dowel diameter (mm)	24	15	9	6	3	bottom	N
<u>Aeshna californica</u> (%)	43	57	0	0	0	0	60
<u>Anax junius</u> (%)	34	43	0	5	4	14	116

complex than that demonstrated by Kime, the preference curve of final instar X. zealandica larvae displaying a distinct discrimination against stems with both too small and too large diameters. The reduced site diameter discrimination of smaller members of a given cohort appeared to be common to both taxa.

It has been postulated that insect larvae can partition a habitat through age specific microhabitat selection (e.g. Werner & Gilliam 1984). A specific suggestion has been that perch diameter could be a partitioning variable, with smaller larvae occupying narrower stems than those preferred by their larger congeners (Corbet 1980). Such a partitioning could reduce the pressure of intraspecific competition on smaller individuals. In X. zealandica, intraspecific agonistic interactions occur across a range of instars, leading in most instances to the displacement of markedly smaller individuals. Smaller larvae would appear to 'need' some form of refuge from larger conspecifics. 'Alternative' sites to the vertical stems, such as roots, bottom detritus or the branches and leaves of macrophytes, do not appear to have any marked attraction for X. zealandica larvae.

My investigation failed to find any marked difference in site diameter preference between different sized instars within a cohort. However, there was some evidence for the preference of different perch size ranges by larvae of different cohorts. Larvae in the 8th and later instars (representing the senior cohort) did not differ in their site diameter preference; whereas those in the 6th and 7th instars

(representing the junior cohort) were more likely to use smaller diameter perches. The use of finer divisions in the stem diameter range 2 – 7 mm may have revealed a more significant pattern of stem diameter preferences. Tubing of the appropriate diameters was not available.

Site utilisation patterns

Diel activity patterns. The occurrence of diel periodicities and circadian rhythms is well documented for the larvae of a number of anisopteran dragonflies (Paulian & Serfaty 1944, Corbet 1962, Mori & Wada 1974, Cloarec 1975), and Corbet (1962) speculated that some Zygoptera might use locomotory feeding at night in contrast to their use of 'sit and wait', ambush tactics through the day. The only investigation of diel periodicity in the activity patterns of zygopteran larvae appears to be that of Crowley (1979) who found statistically significant differences in activity levels between larvae of Ischnura verticalis Say (Zygoptera: Coenagrionidae) feeding under 'diurnal' and 'nocturnal' conditions. The possibility that X. zealandica larvae might remain immobile on perches during the day and then become active at night was investigated.

Although the activity levels of X. zealandica larvae in light and dark conditions differed at a statistically significant level, the biological significance of this difference appears to be negligible. Settled larvae rarely moved, whether in the dark or light, and such movements as did occur were generally trivial. For example, larvae climbed a few millimetres or turned to face in the opposite direction; there was no systematic change in behaviour. It has been suggested that nocturnal movement might be an adaptation to predator avoidance (Corbet 1962, Heads 1985) but it is unlikely that such an interpretation would apply to the minor movements that I recorded. When aquaria were examined at two hourly intervals day and night there was no obvious pattern of between stem movements being nocturnal.

Crowley (1979), using a multifactorial ANOVA design, found Ischnura verticalis larvae had a significantly higher level of activity in the light, but again the biological significance of the differences was unclear.

Moulting. During larval life, X. zealandica larvae undergo a series of moults; typically 11-13. For about 24h prior to and 12h after each moult they do not feed. Moulting is likely to be a time when odonate larvae are under considerable physiological stress and, because of limited mobility, particularly vulnerable. The propensity of larvae to move about their site immediately prior to moulting and to abandon sites immediately after moulting could be a response to a generally heightened stress level associated with the moult.

Emergence. Between the larval and adult life stages, dragonflies undergo metamorphosis as adult structures form within the larval cuticle. A few days before emergence the adult labium retracts from inside the larval prementum leaving the animal to fast until after emergence has been completed (Corbet 1962). Deacon (1979) detected the first external signs of metamorphosis in X. zealandica larvae held at 16°C, a maximum of 12 days prior to emergence. In my study, some animals were seen to attack prey as few as four days prior to emergence but others ceased to feed at least a week before they emerged. In many anisopteran species, pharate adults spend considerable periods of time seeking appropriate emergence sites (Corbet 1962) but small damselflies often seek their sites immediately before emergence, 'in a rather impromptu fashion' (Corbet 1960).

While a few X. zealandica larvae moved to the top of stems some days prior to emergence, this was far from being a general phenomenon. Some larvae even remained on 'roots' (sites providing no possibility of emergence) until hours before ecdysing; behaviour which was matched by

the absence of statistically significant changes in the overall usage of sites by the population as a whole during the period leading up to emergence. Corbet's (1960) conclusion, based on field observations, that emergence site selection is a very rapid process in zygopterans, generally held in the laboratory for X. zealandica.

Habitat usage

The habitats occupied by larval coenagrionids have the potential to be extremely complex when considered on a scale appropriate to the animal. When using 'outrageously artificial ecosystems' (Crowley pers. comm.) there are dangers of 'creating' results which have little relevance to the natural situation. The natural substrates available in a typical pond include roots, stems and leaves of emergent vegetation, floating vegetation and bottom detritus. In this investigation, every attempt was made to provide reasonable facsimiles of natural substrates. Stem and root diameters ranged from about 2 to 11 mm (i.e. encompassing those of Juncus articulatus L., Eleocharis acuta R. Br. and several Scirpus and Typha species) and stem density used was similar to that found in reedbeds. Other substrates - roots, detritus, branches (with and without 'leaves'), facsimile macrophytes and natural plant materials were provided on occasions. Both spatial and temporal dimensions of site use were examined.

Larvae had a strong tendency to remain at the bottom of stem sites, facing the aquarium floor. Relatively little use was made of structures such as branches and leaves; however, some individuals appeared prepared to use, and to stay on, almost any type of site offered. While general patterns were apparent the mysteries surrounding site choice by individuals remain.

Larvae stayed on sites for long periods (up to 82 days (Rowe 1980)). The apparently negative exponential shapes of the duration of occupation data sets indicate a Poisson process with a constant

probability of a site being abandoned. Differences in 'decay constants' for various substrates is a measure of habitat effects on site occupation behaviour. As with second-instar larvae (Chapter 7), the durations of occupation appeared to be a function of site characteristics and not of larval growth rate. If larvae in diapause had not been available it would have been impossible to investigate the temporal pattern of site occupation. Site occupations in excess of 40 days were not uncommon; yet larvae out of diapause complete development well within this time scale.

Prey. No consistent differences in site use by X. zealandica larvae were observed when different prey types were offered. Such differences as did occur were well within the variations occasionally found between two rows of sites situated in the same aquarium. I cannot explain the propensity of larvae to abandon 2-mm diameter stems when fed Lumbriculus. This pattern appeared consistently in a number of aquaria but similar patterns were not found with starved larvae or with larvae fed Lumbriculus but with access to larger diameter stems. Starved larvae displayed stem usage patterns indistinguishable both in microhabitat occupied and in duration of occupation from those of well fed larvae.

Intraspecific interactions. A large repertoire of agonistic behaviours associated with site defence has been documented in X. zealandica (Chapter 2) and larvae often spent considerable periods in territorial disputes. Therefore, the effects of intraspecific interactions needed to be taken into consideration when examining site usage.

Larval densities in the field varied widely. Sweepnetting weed beds in Cass pond produced from about 50 to 200 final and penultimate instar larvae m^{-2} at different times of year and, using a value of capture efficiency obtained from mark-recapture experiments (unpublished), calculated densities ranged from 170 to about $670m^{-2}$. Density

correlated effects (increased intraspecific interactions and general stress effects) needed to be considered. Breakdown of territorial behaviour at high densities is widely documented in dragonfly mating systems (review Corbet 1980, unpubl. obs.) and occurs frequently among animals in general (Wilson 1975).

There was no evidence of a breakdown in territorial behaviour among X. zealandica larvae at high densities. At the highest density tested (160 larvae-m⁻² and two larvae per stem) some individuals obtained and maintained occupant status on sites despite being involved in high numbers of interactions. However, the very high mortality found in the high density aquaria, in contrast to negligible mortality in low density aquaria being operated at the same time, suggests that a high stress level was associated with increasing density.

Austrolestes colenisonis

Austrolestes colenisonis occurs in many of the same habitats as X. zealandica but lacks the complex agonistic behavioural repertoire characteristic of that species (Chapter 2). Use of space by A. colenisonis was examined to provide a contrast with X. zealandica. Larvae of A. colenisonis defend a 'personal space' (Chapter 2) using an agonistic display. They do not, however, localise in one spot for any length of time. Like Lestes disjunctus (Baker 1981b) they appear to forage actively for prey during daylight, and stationary sites would appear to have little importance to them. The occurrence of A. colenisonis larvae on stems at night suggests that stems may be used as some kind of refuge during darkness, when this visual predator (Corbet 1962) would be restricted in its sensory capacity.

Experimental design

During this study, a lot of time was spent investigating stem occupation. Given the impossibility of 'proving' the null hypothesis,

that site selection was indifferent to changing prey species and habitat diversity, it can fairly be asked why I put so much effort into this aspect of the study. The answer lies in the popularity of optimal foraging theory and my original intention to interpret the activity of Xanthocnemis larvae in an optimal foraging framework. Optimal foraging theory and a number of other models make assertions about the expected behaviour of animals; within this context I saw it as important to make a substantial documentation of negative as well as positive evidence.

It is simple to erect a number of 'straw man' null hypotheses which can then be refuted. For example, it can be postulated (H_0) that larvae will be distributed randomly throughout the environment offered, and that the 'time constant' of the system was very much less than the time between observation 'time slices'. A simple Chi-square test would reject this null hypothesis generating three further hypotheses which account for the lack of 'fit':

H_1 : larvae are randomly distributed but time between observations is smaller than (or of the same order as) the time constant of the system (i.e. we are examining historical effects).

H_2 : larvae have preferred sites but time between observations is much greater than the time constant of the system.

H_3 : larvae have preferred sites and time between observations is smaller (or of the same order) as the time constant of the system.

H_0 asserts larvae will be randomly distributed and that the sampling scheme is unbiased. H_1 asserts the data is correlated because of repeated sampling of the same spatial distribution. H_2 asserts the sampling scheme is valid but that correlation occurs through non-random behaviours of the animals. H_3 asserts both effects (H_1 and H_2) occur.

While consistent with behaviour in newly occupied aquaria, in long term 'free range' aquaria H_2 can be rejected on the basis of duration of occupation data. H_1 can be rejected because of the consistency of larval responses across a large number of aquaria (the aquaria being independent experiments). This leaves H_3 , in which the sequence of 'time slice' observations become an examination of the behaviour of larvae on stems. The larvae proved to be remarkably inactive.

There are statistical difficulties with all time series analyses through the lack of independence between successive observations. The data obtained in this investigation involved a large number of larvae over a long period of time. Throughout the experiments larvae were free to adjust their positions at any time. If the Markov assumptions are met the animals will gravitate towards their steady state distribution; thereby providing a measure of site preference. It is thus possible to appeal to the law of large numbers and regard the accumulated frequency distribution as a representation of the steady state distribution. The close similarity of the data sets from different aquaria show that there is consistency in the behaviour of the larvae, even if this pattern cannot be evaluated by statistical methods. X. zealandica larvae spent most of their time on perches, generally head down at the bottom of stems. This behaviour did not alter in response to prey species behaviour, or in response to hunger (within limits!).

X. zealandica larvae are sedentary throughout their larval life. They are sit and wait, ambush predators which prefer to use sites in a certain range of diameters which are raised above the floor of the aquarium (or pond). Preferred sites are occupied for long periods of time (often for a large portion of an interstadial) and even non-preferred sites may be occupied for very long periods of time. Site occupation appears largely indifferent to the food regime offered. Larvae are known to be territorial (Chapter 2) and they are typically overdispersed on

sites (Rowe 1980). The preference for specific types of site, the territorial defence of these sites and the apparent insensitivity of site occupation behaviour to feeding success indicate that the sites used have some specific adaptive value unrelated to predatory activity.

Section 5: utility

It has been shown that X. zealandica larvae have a large repertoire of agonistic behaviours, associated with defence of a territorial site (Section 2). It has been shown that X. zealandica larvae are competent, sit and wait predators in which hunger stress is probably very rare in the field (Section 3). It has been shown that X. zealandica larvae prefer certain types of territorial site and remain on sites for long periods (Section 4). Site use appeared insensitive to changes in feeding regime.

Explanations of the territorial behaviour of X. zealandica larvae in terms of defending a 'fishing site' did not fit with the evidence obtained. Possible alternative selection pressures which would give the sites adaptive function needed to be sought. In this section the use of the territorial perch as a refuge from predators is examined.

CHAPTER 9

Xanthocnemis zealandica territorial sites -

refuges from predators

INTRODUCTION

Territorial behaviour is widespread in the animal kingdom (Wilson 1975) and the adaptive significances of observed territorial behaviours are of considerable interest (e.g. Hinde 1956, Wilson 1975, Krebs & Davies 1978). Reviews (Wilson 1975, Krebs & Davies 1978, 1984, Baker (R.R.) 1983, Fitzpatrick & Wellington 1983, Kaufmann 1983) have largely emphasised the benefits of territorial behaviour in controlling or obtaining access to 'consumable' resources (specifically mates and food) important for promoting the fitness of the individual. A considerable literature has developed wherein territorial behaviour is subjected to cost/benefit analysis under the assumption that access to some consumable is controlled (review Krebs & Davies 1978, 1984, Kacelnik et al 1981, Davies & Houston 1981, Martindale 1982). An alternative function, the defence of a refuge from predators (Hinde 1956), has received attention recently as a potential adaptive benefit of territorial behaviour in fish (Phillips & Swears 1979, Grossman 1980) and juvenile lizards (Stamps 1983).

As a subject for investigating territorial function larval Xanthocnemis zealandica (McLachlan) (Odonata: Coenagrionidae) have a number of advantages. They are territorial, 'sit and wait' predators, generally taking 2-3 years to develop, and have a diapause stage in which development can be suppressed (Deacon 1979, Rowe in press). They exhibit preferences for specific site geometries and remain on the same site for long periods (Chapter 8). Sites are defended from conspecifics

using an extensive and complex repertoire of agonistic displays (Chapter 2). As larval insects they have no involvement in breeding activities and their territorial site occupancy is insensitive to hunger levels (Chapter 8); hence defence of predation refuges would appear to be a likely function of the observed territorial behaviour.

In this investigation final-instar X. zealandica larvae were placed in aquaria with potential predators and the effect of stem presence on survival measured.

METHODS

The potential predator selected for use in laboratory experiments was the adult stage of R. pulverosus. Adult beetles are easy to maintain, long lived and, unlike the rapidly growing larval stage, are not susceptible to changes in behaviour associated with metamorphosis. They occur in the same habitat as X. zealandica and laboratory studies have shown that both adult and final-instar R. pulverosus larvae subdue and prey on final-instar X. zealandica larvae with ease. R. pulverosus adults are voracious foragers which scour shallow water habitats for available prey and even at densities very much higher than those used here there appears to be no interference between beetles (W. Dowdle pers. comm.). Carcasses of X. zealandica eaten by beetles have an unmistakable appearance with flaccid areas lacking supporting tissue separated by pale lumps of coagulated protein. The characteristic remains left after predation prevent any possibility of losses during experiments being ascribed to cannibalism on the part of the dragonfly larvae (there are allegations in the literature that larval Odonata are cannibals – but see Chapters 5, 6). The behavioural responses of X. zealandica larvae to beetles were examined on videotape recordings.

Standard 25 x 40 x 15 cm deep aquaria were set up in a 16°C constant temperature room under a 12h light/12h dark regime. Each

aquarium contained 8 X. zealandica larvae in penultimate or final instars and either one or two R. pulverosus adults. Tests were conducted with or without refuges present and with two different water depths: 5 cm or 10–12 cm. In all but three trials the refuges provided were vertical, wire supported, 'stems' of stiff polyethylene tubing 4.5 mm in diameter. A size and geometry preferred by larvae in earlier choice experiments (Chapter 8). The remaining three trials were done using the less preferred, 2 mm diameter stems. Twelve stems were offered to reduce the potential for interference inherent in the territorial behaviour of the damselfly larvae.

Aquaria were set up and left for 24h after which killed larvae were counted and replaced. The alternative stem condition (i.e. stems were removed from aquaria which had had refuges and vice versa) was then imposed. This procedure produces a systematic bias against stems having an effect because the time at risk was calculated from shake off until the reintroduction of stems to the aquarium. As there was no way to ensure that animals remained on stems this bias had to be accepted. After the completion of an experiment the system was run for several days with the stems in place to check for any periodicity in predator success. A systematic experimental protocol was chosen, rather than a randomised design, to minimise the number of prey required and to prevent distortions due to short term fluctuations in predator food requirements (as e.g. accompanied oviposition in a trial run) given the limited number of replicates available.

R. pulverosus was willing to attack potential prey throughout the experiment.

To reduce the influence of differences between beetles, results were analysed as sequential pairs using the signs test.

Additional observations were made with larval R. pulverosus, larval Aeshna brevistyla Rambur (Anisoptera: Aeshnidae) Anisops sp. (Heteroptera: Notonectidae) and Sigara sp. (Heteroptera: Corixidae) as potential predators.

RESULTS

Behavioural observations

Prey capture by Rhantus

On three occasions, Rhantus was observed capturing X. zealandica larvae. In each case the beetle was swimming immediately above the floor of the aquarium and appeared to 'bump into' a larva travelling in the same direction. Rhantus seized the larva with its first and second pairs of legs, floated into midwater and eventually to the surface, gnawing at the prothorax/neck region of the larva. For about 30-60s the larva made swimming movements but then ceased struggling. The beetle floated at the surface for some minutes feeding on the dead larva which was finally dropped. Rhantus swimming over the floor of an aquarium frequently seized Xanthocnemis carcasses, carried them to the surface and fed. Most carcasses were fed on many times with chewing concentrated on the abdomen near the junction with the thorax. Rhantus may be aided in their search for carrion by an ability to follow a chemical gradient (Richard, cited in Cloarec 1972).

Rhantus larvae were also observed attacking X. zealandica larvae. On contacting a damselfly larva the beetle larva spread its mandibles widely and directed itself towards the point of contact. If a further contact was made, Rhantus lunged forward and snapped its mandibles closed. It seems likely that some form of venom is injected as the prey ceased moving very quickly. The Rhantus larva then moved to the surface and consumed the prey, repeatedly adjusting the position of

the carcase with its legs and making a series of incisions along the body of the prey.

Antipredator responses of X. zealandica larvae:

Larvae on stems almost invariably responded to approaching R. pulverosus adults by 'squirrelling' around their support, interposing the stem between the predator and themselves (rapid lateral movement of Chapter 2). Responses occurred typically at a separation of 5–15 mm and the average angular speed of the escape movement around a 4.5-mm diameter stem was in excess of $470^\circ/\text{s}$ (as shown by videotape recordings). Larvae often 'bounced back', with the same speed, to their original position as the Rhantus passed by (Fig. 67). When Rhantus was resting alongside, or even touching, a larva, the latter did not move until the beetle had swum off. When Rhantus swimming over the bottom of the aquarium came across and attempted to grasp larvae, most of the Xanthocnemis wriggled free and swam off.

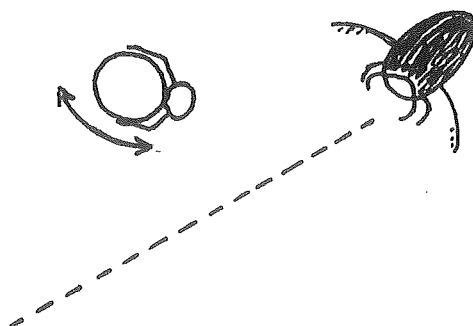


Fig. 67. Response of X. zealandica larva to a passing R. pulverosus beetle. Arrows indicate the direction and extent of the larval movements (elapsed time about 0.5s).

No specific, active response to the presence of Rhantus larvae was observed. However, many of the X. zealandica larvae climbed the walls of the container until they were above the water level (normally a most exceptional behaviour), while others clung to small fragments of waterlogged twig. Rhantus larvae appeared to be unable to attack X. zealandica larvae successfully on the vertical walls of a container. The capture success of Rhantus larvae increased when all scraps of twig had been removed from a container and after Xanthocnemis larvae had been forced back into the water. One X. zealandica larva was seen being grasped by a Rhantus larvae which appeared to be seeking a support so it could remain underwater. The damselfly larva remained still as the pair floated to the surface and, although it was in a contorted position (Fig. 68), did not move again until released by the beetle larva. When the Rhantus had finished taking in air it released the Xanthocnemis and dived; the Xanthocnemis immediately swam vigorously to the bottom.

Aeshna larvae seemed able to recognise motionless Xanthocnemis larvae in the cryptic posture (Chapter 2) and stalked slowly towards them. When attacked from behind, Xanthocnemis larvae made no attempt to break free by thrashing about but instead used their legs in an attempt to drag themselves away along the stem on which they were perched. When attacked from in front they were torn from the stem and were dead within seconds.

Anisops sp. (Heteroptera: Notonectidae) and Sigara sp. (Heteroptera: Corixidae), potential predators which swim in midwater were ignored or even, on occasions, stalked and (unsuccessfully) attacked by final instar X. zealandica larvae. This response was surprising as both heteropteran species had been observed in the laboratory preying on earlier instar X. zealandica larvae (up to the 10th of 12-14 instars). Swimming X. zealandica often elicited the rapid lateral movement response (Chapter 2) from perched conspecifics.

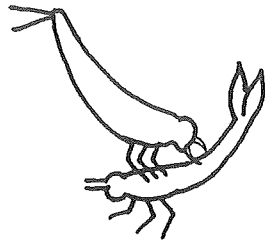


Fig. 68. X. zealandica larva 'freezing' while held by Rhantus larva.

EXPERIMENTS

Effect of water depth

Adult Rhantus were ineffectual predators in aquaria with water 10–12 cm deep. They appeared to have difficulty searching the bottom of the aquarium and two groups of 8 larvae on stems each exposed to Rhantus for 24 hours suffered no casualties. After a further 48h exposure with the stems removed two X. zealandica were dead but only one had been attacked by a Rhantus. Nevertheless Rhantus attacked lumbriculids (Annelida) at the termination of each experiment. This result was surprising in view of observations of Rhantus behaviour in ponds where they forage through bottom detritus at depths of 30–40 cm. A lack of sites where submerged beetles could cling and rest may have been the reason for this lack of feeding. This problem could not be solved without providing X. zealandica with unwanted potential refuges so the experiment was reorganised using a water depth of 5 cm. Rhantus proved able to forage at this depth without bottom resting sites.

Effect of stems on X. zealandica larval survival

In 5 cm of water Rhantus adults proved able to capture X. zealandica larvae. Tests were run using 2 mm diameter (non-preferred) and 4.5 mm diameter (preferred) stems. Under the test conditions there appeared to be little difference in predation success between the two types of stems ($X^2 = 0.01$, ns) and for logistic reasons subsequent trials were done with 4.5 mm diameter stems.

Table 26. Predation on X. zealandica larvae by R. pulverosus beetles in 5 cm of water; stem diameter 4.5 mm. Eight larvae were exposed to two beetles and the losses (beetle)⁻¹ recorded.

with stems	0.5	0.5	1.5	1	1	2	0	0	0	0.5	0.5	0.5	0.5
without stems		2	1	2	1.5	1.5	2.5	2	1.5	2			

Table 27. Predation on X. zealandica larvae by R. pulverosus beetles in 5 cm of water; stem diameter 2 mm. Eight larvae were exposed to 1 or 2 beetles and the losses (beetle)⁻¹ recorded.

with stems	0	2	1.5
without stems	5	5	2.5

The improved survival associated with the presence of stems was highly significant ($P \leq 1/2048$, 2-tailed signs test on sequential pairs). Pooling the data and using the Mann-Whitney U-test $P \leq 0.001$ (2-tailed) ($U=174$, $N_1=16$; $N_2=12$).

In contrast to X. zealandica, final and penultimate instar larvae of Austrolestes colensonis (White) (Odonata: Lestidae) kept in similar aquaria appeared to be immune from predation by adult R. pulverosus. Size, strength and their rapid, swimming, escape response were factors in this immunity. This was in marked contrast to the known vulnerability of A. colensonis in the field (Dowdle 1981).

DISCUSSION

The concept of a territory as an antipredatory adaptation can probably be attributed to Hinde (1956) who crystalised some arguments of Tinbergen. Hinde stated with reference to nesting birds '...although no direct evidence is available, circumstantial evidence suggests that territorial behaviour will reduce predation in species with cryptic eggs, nests or females'. This line of argument does not appear to have been developed to any great extent. Instead, most modern investigations of territorial behaviour have concentrated on cost/benefit analyses of the protection of consumable resources. Davies (1978) and Kaufmann (1983) both cite the work of Black (1971) on sticklebacks (Gasterosteus aculeatus) and Krebs (1971) on Great Tits (Parus major) as evidence for territories being used to avoid predation. In both these examples, and others considered by Hinde, the benefit of the territory appears to be through the protection of helpless progeny from predators which are of little danger to the territory holder. They are not for the defence of a refuge for the protection of the territory holder.

Philips and Swears (1979) and Grossman (1980) demonstrated that some fish defend what are apparently refuge sites, and showed that those with refuge sites had a higher survival expectation against predation. In Grossman's example the issue of function is confounded because the burrow defended served also as a refuge from environmental stress. Stamps (1983) working with juvenile lizards, which are susceptible to predation by lizards and birds, documented defence of home sites apparently unrelated to food availability and a preference for 'complex' sites, especially in the presence of 'predators'. In Stamps' investigation, anti-predator behaviours were observed which utilised the features of 'complex' refuges and resulted in predation success on lizards both in the field and in the laboratory being low.

There are few potential predators of X. zealandica in New Zealand's endemic fauna. However, the fauna suffered extensively during the Pleistocene (Chapter 1) and we have little idea of the faunal composition of ecosystems in which X. zealandica evolved. Of the extant native fishes the bullies (Pisces: Eleotridae) Gobiomorphus breviceps (Stokell) (Staples 1975) and Gobiomorphus cotidianus McDowall (R. Naylor pers. comm.) occasionally take X. zealandica larvae and an unidentified zygopteran larva has been recorded in gut contents of Galaxius argenteus (Gmelin) (Galaxiidae) (Jellyman 1979). M. Main (pers. comm.) has recorded final instar X. zealandica larvae and pharate adults in G. argenteus from coastal lakes in Westland. Native fish, especially galaxiids, have been suppressed during the last century by trout introduced to many New Zealand freshwaters (McDowall 1978), and hence it is difficult to estimate how intense fish predation pressure would have been on X. zealandica in evolutionary time. Trout (Salmo spp.) do consume numbers of X. zealandica larvae, but in the main they catch pharate adults (J. Hayes pers. comm.; own unpubl. obs.).

Invertebrate predators of X. zealandica larvae include larval dragonflies (Aeshna brevistyla Rambur and Hemianax papuensis (Burmeister) (Odonata: Aeshnidae)) and adult and larval Rhantus pulverosus (Stephens) (Coleoptera: Dytiscidae) (unpubl. obs.). The aeshnid species are sparsely distributed but sometimes locally abundant in New Zealand ponds; both are probably Australian colonists (Rowe in press). R. pulverosus is a cosmopolitan species common in New Zealand ponds.

Stamps (1983) claimed that to demonstrate the protective function of territoriality it is necessary to: (1) identify predators in the field; (2) show that predator refuges are in short supply in the field; (3) show that prey defend refuge sites and (4) show that refuges confer protection against identified predators.

In my study, potential predators identified in the field included fish (eleotrids, galaxiids, salmonids) and insects (aeshnids, dytiscids); however, examinations of gut contents indicated that only the aeshnid H. papuensis preyed extensively on larval Coenagrionidae. Susceptibility to predation by aeshnids may be widespread among coenagrionids. Lawton (1970) noted that Pyrrhosoma nymphula (Sulzer) was readily preyed upon by Aeshna cyanea Muller (Odonata: Aeshnidae) larvae in the laboratory and that numbers of coenagrionid larvae appeared to be depressed in the field when A. cyanea was present. In contrast, Griffiths (1973) did not record P. nymphula in the diet of Aeshna juncea (L.). Folsom & Collins (1984) found both Enallagma and Ischnura (Coenagrionidae) in the faecal pellets of Anax junius Drury.

In New Zealand introduced Salmo species consume large numbers of pharate adults and the seasonal occurrence of X. zealandica in Staples' (1975) G. breviceps samples indicate that these too were probably in this life history phase. Pharate adults would become vulnerable to predators after they abandon their territorial perches on submerged deep-water vegetation to seek emergence sites.

Stamps' second criterion, that refuges (or good refuges) must be in short supply is far too restrictive. Many predators are known to use localised search patterns in the vicinity of detected prey, following predatory success or in habitats which correlate with prey availability (review Curio 1976). Conspecifics in close proximity could potentially attract predators to the site, undetected by the senses of non target animals. Such searching predators would be extremely dangerous to unsuspecting individuals. Thus even when 'refuges' are superabundant there is still adaptive value to prey animals in keeping other individuals away from their immediate vicinity. Only if the refuges are invulnerable is the distribution of conspecifics inconsequential. That is, when the occupation of refuges alters the marginal probability of

successful evasion of predators prey may further increase their probability of survival by ejecting conspecifics from the area.

Under certain circumstances, X. zealandica refuges (stems) may be in very short supply (with final and penultimate larval densities sometimes reaching $> 600 \text{ m}^{-2}$); however, it would seem that under 'normal' conditions refuges are abundant if not superabundant. In the laboratory, X. zealandica larvae spend much of their time in refuges (Chapter 8) and the limited larval mobility in the field (unpubl. results) is consistent with this finding.

An extensive repertoire of intraspecific agonistic displays is used by X. zealandica larvae to defend their perches from conspecifics (Chapter 2). The elaborate system of displays and the time spent defending perching sites (with the assumed consequent opportunity cost vis a vis feeding - e.g. Thompson 1978a, Uttley 1980) indicates that these sites have some major significance in the life history of the animals.

My observations showed that perches and perch associated behaviours conferred protection against both larval and adult dytiscids but not against aeshnids. The presence of perches produced a statistically significant degree of protection against adult Rhantus in the laboratory. In choice experiments (Chapter 8), X. zealandica larvae preferred stems with a circumference slightly greater than twice the larval leg span. This stem size permits a high angular speed and provides a large 'shading' effect to hide the larva.

The efficacy of the predator refuges used by X. zealandica could account for its being underrepresented in the diet of R. pulverosus in the field. The prey of R. pulverosus adults and larvae in Remus pond at Cass, the main source of X. zealandica for this investigation, were determined by Dowdle (1981). R. pulverosus, A. colenisonis and X. zealandica occupied the same areas and utilised the same habitats in

similar numbers but few X. zealandica were eaten. W. Dowdle (pers. comm.) detected X. zealandica in only 2 of 145 R. pulverosus larvae she examined serologically, whereas A. colenisonis was present in more than 60 animals. Zygopteran remains were found in 5 of 52 adult R. pulverosus, but none were positively identified as X. zealandica. This result probably underestimates the impact of adult beetles as Dowdle was searching the gut contents of adult beetles for sclerotised remains. Given the relative immunity to predation of final and penultimate instar A. colenisonis larvae in the laboratory it is probably the earlier instars that are suffering the brunt of this predation pressure in the field.

There have been few studies of microhabitat selection and use by either dragonfly larvae (section 4) or other 'sit and wait' predators. The adaptive significance of the site selected is a largely neglected question as it has been tacitly accepted that the sites must be predation sites. The use of sites in the predatory activity of coenagrionid larvae has been investigated by Crowley (1979) (Ischnura verticalis Say) and Baker (1980, 1983) (Coenagrion resolutum (Hagen), Ischnura cervula Selys). Baker examined activity on a dowel lattice and occupation of the single feeding site provided over a period of 10 days. In both C. resolutum and I. cervula he found that single animals located, and remained at, the feeding site and that when several animals were on the apparatus there was a disproportionate usage of the feeding site by some individuals. This was interpreted as indicating a dominance hierarchy and exclusion of lower ranked animals. This site usage contrasts with Baker's (1981) findings on Lestes disjunctus Selys (Odonata: Lestidae) which did not remain near the food source or utilise the dowel lattice to any extent. The behaviour of L. disjunctus is very similar to that observed in A. colenisonis (Chapter 8). Crowley examined the use of a (different) dowel lattice by individual I. verticalis during their

first hour of occupancy. He found that larvae moved very little.

X. zealandica also uses its perch as an ambush site for predation but appears reluctant to move from the perch even when hungry (Chapter 8). Nearby prey is approached by the larva releasing its fore and middle legs from the perch and 'stretching' toward the potential prey while holding firmly with the hind legs. Larvae settled on stems will leave them briefly to scavenge nearby carrion which is dragged back to the stem (Chapter 5).

There is a temptation to interpret the behaviour of predators solely in terms of their predatory activities. In animals such as R. pulverosus larvae (average daily biomass increase 20%, unpubl. obs.), Pantala hymenaea (Odonata: Libellulidae) (average daily biomass increase 20%, from Corbet 1962), Ischnura aurora (Odonata: Coenagrionidae) (average daily biomass increase 16%, from O'Farrell 1970), H. papuensis or A. colenisonis (average daily biomass increase 8%, unpubl. obs) there may be some justification for regarding other aspects of their ecological tactics as being relatively unimportant. However, in cases where animals are slower growing despite occupying similar habitats and eating similar prey to (some of) the above (e.g. X. zealandica, Procordulia smithii (Odonata: Corduliidae), A. brevistyla - average daily biomass increase 1 - 3%, unpubl. obs.) predation is unlikely to be their dominant activity.

Larval insects do not partake directly in reproduction. However, there are two factors which markedly affect their potential fitness: eating and the prospect of being eaten. Conventional wisdom concentrates on the first factor. It is postulated that maximal foraging with high growth rates minimises the period at risk through rapid development and further improves fitness by increasing adult size (within the range of the species) hence increasing intrasexual competitiveness and/or fecundity (Lawton et al 1980). On the other hand it is obvious that

animals which avoid being eaten, survive, and so get the opportunity to breed. An animal which is a less efficient predator can be expected to have a reduced expected fitness for a variety of (largely indirect) reasons (Lawton et al 1980). How important this is in view of the stochastic nature of the habitat is unclear (Benke & Benke 1975 found 80% mortality between the beginning of metamorphosis and emergence, and losses may also be high during the prereproductive period (Parr 1973)). An animal which is eaten suffers an immediate, catastrophic and total loss of fitness.

Two distinct life history 'solutions' appear to have evolved in the Odonata (Johnson & Crowley 1980). Some species (e.g. Anax (Kime 1974), Hemianax (O'Farrell 1970), Lestes (Corbet 1962), A. colenisonis and I. aurora) have very high growth rates and thus pass through the predation-susceptible stage quickly. Others (e.g. Aeshna (Kime 1974), X. zealandica) develop more slowly, are cryptic and evade predators. Species in the first group tend to use ephemeral habitats (thereby escaping predators in space and/or time) as well as permanent habitats; those in the second group are restricted to more or less permanent habitats.

This dichotomy of life history tactics is a consequence of the temperate environment. For a self sustaining population:

$$P(\text{survive larval phase}) * P(\text{survive to sexual maturity}) * \text{fecundity} = \underline{0(1)}$$

Within a family phylogenetic constraints impose basic similarities on fecundity and adult survival to sexual maturity. Thus it is reasonable to assume that fecundity is proportional to size and $P(\text{survive to sexual maturity})$ is almost independent of species (given the close similarities in adult life during maturation in dragonflies) within a family. These assumptions may hold more generally across wider taxonomic units.

In Odonata mortality is nearly constant throughout larval life, but rises sharply at the onset of metamorphosis (Benke & Benke 1975). Under these conditions it follows that the probability of surviving the larval stage must also be almost equal across species. Larval survival can be decomposed in terms of the daily marginal survival expectation:

$$P(\text{survive larval phase}) = (P(\text{daily survival}))^{\text{days at risk}}$$

$$P(\text{survive larval phase}) = x^y$$

The solution set to this is $x, y \quad 0 < x < 1, y > 0, x^y = k \text{ (fixed)}$. Under temperate conditions y is constrained to fall discretely into 0, 1, 2, years. This and the sensitivity of the function produce an apparently discrete spectrum of feasible tactics (Table 28). With realistic larval survivorship (0.01 – 0.05) species which pass through their larval life in a single season (30, 50, 90 days) can withstand a daily loss of 3–10% whereas those taking a year or more to complete larval development require a daily loss rate below 1%.

Table 28. Tabulation of daily survival rates necessary to produce given larval life survival values.

days at risk	30	50	90	250	300	600	900
survival							
0.05	0.90	0.942	0.967	0.988	0.99	0.995	0.997
0.01	0.79	0.871	0.926	0.973	0.977	0.989	0.992

Andrews (1979), discussing a 'sit and wait' predatory lizard stated that lizards were themselves under considerable predation pressure in the tropical forest. On the basis of his own difficulties in detecting the animal he argued that other visual predators would encounter similar difficulties and that the 'sit and wait' tactic was associated with predator avoidance. It may be that 'sit and wait' predators are preadapted for predatory avoidance territoriality and therefore this may

be a widespread function of territorial behaviour.

The conventional explanation for coenagrionid larval perches solely as 'fishing sites' (Macan 1964, 1977; Thompson 1978a) clearly is open to doubt, at least in X. zealandica. Larvae remain on their perches even when maintained under considerable hunger stress (in terms of expected feeding rates in the field) and starved larvae do not readily abandon their stems to pursue food. There is no evidence that the sites selected and defended have any attractive properties for prey. Sites and associated site usage behaviours provide an effective counter to at least one of the predators commonly found in X. zealandica's larval habitats. Site occupation and usage by other long-lived coenagrionid larvae may also be governed by predator avoidance and refuge defence may be widespread in this family.

CHAPTER 10

General discussion

The principal aim of this thesis was to discover how the actions of individual dragonfly larvae determine patterns of site use and thereby to provide a basis for the interpretation of some aspects of traditional ecological studies of these predatory insects. The approach taken was to follow individually marked Xanthocnemis zealandica larvae for months at a time as they moved about large (25 x 40 x 15 cm deep) aquaria in which a variety of different potential perches were offered. Detailed observations were made of intraspecific contests both in the large aquaria and in small (15 x 4 x 15 cm deep) ones where interactions were induced by limiting the number of perch sites and by crowding. Predation and predator avoidance behaviours were investigated in both large and small aquaria. Activities of early instar larvae were investigated in smaller sized containers.

I found that X. zealandica larvae were cryptic, sit and wait predators throughout their larval lives. Later instar larvae showed strong preferences for certain types of site and remained on particular perches for long periods. A large repertoire of displays was involved in the agonistic behaviour X. zealandica larvae used to defend their sites from conspecifics. Comparative studies were made of site use by, and agonistic behaviours of, Ischnura aurora and Austrolestes colenisonis to find to what extent my findings on X. zealandica could be used as a more general model of dragonfly larval behaviour.

The ecologies and behaviours of many predators have been investigated extensively. This has been a response in part to an intrinsic interest in the animals in their own right, and in part to an intuitive belief that predators have a role in determining population

structures in ecosystems. For long the second consideration was an act of faith as, except in restricted habitats and on occasions when new predators were introduced into previously isolated ecosystems, there was little concrete evidence of predator influence on prey populations (review Glasser 1979). Recently, with the realisation that predators may place disproportionate pressures on certain vulnerable life history stages, evidence of predator structured populations has been found in a variety of disparate ecosystems (e.g. Benke, Crowley & Johnson 1982, Bergerud 1983). The potential impact predators can have on prey populations is to a great extent dependent on the detailed structure of their prey capture behaviours (Huey & Pianka 1981). In this context the activities of sit and wait and ambush predators are especially interesting. Insects constitute about 75% of animal species (Southwood 1978) and a high proportion of insect predators use sit and wait or ambush tactics. Through their enormous numbers, insects represent an appreciable proportion of the biomass of most non marine ecosystems and the major predators on insects are other insects. Hence the importance of understanding sit and wait predators and ambush predation. As mentioned (p140) there is sometimes confusion between the terms sit and wait and ambush. There should not be.

Predatory behaviours

When analysing predatory behaviour it is important to distinguish between behaviours prior to the detection of prey (the search phase) and behaviours involved in prey capture (the prey attack phase). The search and prey attack phases of predation are triggered by different cues, involve different motor patterns and have different end points.

Before prey is detected, the dynamics of the interaction are determined by the detectability of the prey and the relative motion of predator and potential prey. For any fixed prey detection range the

volume searched in a given time is dependent on the relative motion of predator and prey. Search tactics range through a continuous spectrum from extreme sit and wait predators, where the relative motion is due entirely to prey movements, to active foragers, where predator movement makes a significant contribution to the relative motion. Animals which typify the sit and wait predatory strategy include cobweb spiders, tiger beetle larvae, antlions and anemones. Active foragers, animals at the opposite extreme of this spectrum of prey searching activity, spend much of their time moving about, apparently seeking prey. Pelagic fish, lady bird larvae, foraging crabs, vultures and wolves represent this end of the spectrum. For simple geometric reasons, active foragers have a greater probability of encountering potential prey in any time interval than do sit and wait predators. Encountered prey and vulnerable prey are not necessarily the same thing. Prey attack may be possible only within a limited range of (predator-prey) relative velocities.

Once a predator has detected a potential prey item, attack rather than searching components of the predatory repertoire become involved. In a similar fashion to the search component, prey attack spans a broad spectrum of behaviours. At one extreme are ambush predators which wait for prey to approach within strike range, at the other extreme are cursorial hunters which run their prey down. Ambush predators may make positional adjustments (which generally involve orienting their bodies, or maintaining sensory contact with the prospective prey) and other inconspicuous, low energy cost movements as potential prey approach to within a short range, then strike. The ambush behaviour pattern is exemplified by tiger beetle larvae, antlions, many dragonfly larvae and many of the big cats. At the opposite end of the attack behaviour spectrum from ambush predators are cursorial hunters, animals which run their prey down using behaviours which are unconcealed and involve a high energy cost relative to the equivalent behaviours of ambush predators.

Such predators are exemplified by wolves, wolf spiders and adult tiger beetles. While individual predators may vary their prey acquisition behaviour with changes in age, hunger level, prey type and density, and habitat structure, most predator species can be assigned to a characteristic position on the search behaviour x attack behaviour space (Fig. 69).

There has been an unfortunate tendency, more especially in British literature, to treat 'sit and wait' and 'ambush' as if they were synonyms and to use them interchangeably (e.g. Giller 1982, Lawton et al 1980, Heads 1985). This is incorrect as search behaviour (the sit and wait - active forager spectrum) and attack behaviour (the ambush - cursorial hunter spectrum) represent two different behavioural dimensions. Like 'territory' the concept of 'sit and wait' is most naturally associated with some definite spatial position. A small falcon sitting on a vantage point waiting for prey to come within range is an ambush predator; if the vantage point used is the only site from which ambush attacks are launched then it is also a sit and wait predator; a kingfisher which moves from pool to pool and at each perches at a vantage point waiting for prey to appear is an ambush, but not a sit and wait predator. Similarly, a notonectid which swims about actively when prey densities are low, and appears an archetypal active forager, does not become a sit and wait predator when, at high prey densities, it floats at the surface and attacks from ambush (Giller 1982).

Under the conditions used in this investigation, all X. zealandica larval instars, and all Xanthocnemis sobrina larvae after the second instar, behaved as archetypal sit and wait, ambush predators. Under the same conditions both Ischnura aurora and Austrolestes colensonis proved to be ambush predators but differed in their levels of searching activity; both were more active foragers than was X. zealandica. It is apparent that the position of any species on the sit



Fig. 69. The foraging tactics and prey attack behaviours of a variety of predators on mobile animals (sources various).

and wait – active forager and ambush – cursorial hunter axes must be determined by observation.

Analysis of predatory tactics using OFT

Since the mid 1970s, analysis of both predatory behaviours and the behaviour of predators has come to be dominated by optimal foraging theory (OFT) and it was my original intention to analyse the behaviour of X. zealandica using OFT techniques. However, it soon became apparent that difficulties arise when attempting to analyse behaviours within an OFT framework. A number of the more articulate promoters of OFT differ in their interpretation as to what constitutes OFT – and denunciations for heresy are not uncommon. Further, there appear to be serious mathematical, biological and philosophical difficulties with OFT. Krebs et al (1983, p167) regarded OFT as a programme which will in time subsume other optimality models (life histories, mating strategies, territorial defense (sic)); whereas Pyke (1984) in a subsequent review followed the traditional line that OFT is a theory of foraging behaviour. In their section entitled 'What is OFT?' Krebs et al (1983) started by stating that 'OFT is an attempt to find out if there are any general rules about what animals feed on, where they go to feed, and how they search for food.' They then proceeded to cite examples of 'OFT' studies with no further indication of the underlying assumptions. In perhaps the clearest statement of the assumptions underlying the OFT programme, Pyke (1984) listed the following: 1) fitness is dependent on behaviour while foraging; 2) there is a heritable component of foraging behaviour; 3) the relationship between foraging behaviour and fitness is known; 4) evolution of foraging behaviour is not limited by genetic constraints; 5) evolution of foraging behaviour is subject to realistically determined functional constraints and 6) foraging behaviour evolves more rapidly than the rate at which relevant environmental conditions change. Pyke's first assumption is more correctly stated (Schoener 1971) as a

requirement that fitness is sensitive to changes in foraging success and that changes in foraging success are reflected by changes in fitness.

OFT has had some successes in describing the behaviours of small homeotherms, animals which largely fulfil the assumptions behind the programme. The method has been less successful when applied to other types of animal, and recently even some of the successes on small homeotherms have been challenged (Symposium, Brown University R.I., R. Gray pers. comm.).

While OFT has been occupying centre stage an alternative philosophical position, that of satisficing (Simon 1956) has remained in the wings. Under OFT, natural selection is regarded as being an optimising programme that, over time, will 'generate' life forms which (for their given phylogenetic constraints) will be optimally adapted to their environment. Such an optimal form is an ESS as there will be no errors of exploitation which can be used to invade its niche. Satisficing in contrast holds that natural selection acts until the life form achieves an adequate 'solution' to current environmental pressures. Once such a 'solution' is achieved selection pressure is monotonically reduced until its effects are lost among the stochastic fluctuations which affect individual fitness. There is a philosophical chasm between optimisation programmes (with their sense of perfection) and satisficing (based on adequacy) (Krebs & McCleery 1984). Yet, despite fundamental differences in concept, the programmes may not be experimentally distinguishable (Myers 1983). Satisficing is less elegant mathematically than OFT, makes fewer assumptions and consequently produces weaker predictions. But biologically adequate optimal solutions (if they exist – and this is NOT proved) are contained in the satisfactory solutions. Krebs et al (1983) attempt to invert this and claim satisficing is contained within optimisation (Myers 1983). This is logically impossible. As satisficing requires fewer assumptions than OFT and the predictions made are probably

indistinguishable by experiment, Occam's razor would require us to accept the satisficing programme.

An alternative position has sprung up which, while recognising the difficulties with OFT, holds that OFT terminology and structure provide a useful framework for expressing questions in behavioural ecology (Heinrich 1983, Glasser 1984). In this scheme no attempt is made to use OFT as a predictive (i.e. scientific) device but instead it is regarded as a source of vocabulary and of taxonomies of behaviours.

Coenagrionids are the most successful family in the Zygoptera both in species and individual numbers. Coenagrionid larvae are often extremely abundant in the weed zones of lentic and slow lotic systems. In some habitats they represent the dominant macroinvertebrate predator both numerically and in terms of biomass. For a variety of practical reasons they provide attractive subjects for investigating insect biology. Previous studies of coenagrionid larvae have concentrated on seasonal regulation, larval population structure, broad patterns of larval distribution in the field and feeding activity.

In a number of investigations (e.g. Thompson 1978a, Uttley 1980, Crowley 1984 and Heads 1985) the behaviour of Zygoptera larvae has been interpreted in terms of maximising the rate of food intake. Thompson interpreted the caudal swinging he observed as a ventilatory activity whereas I found these behaviours to be part of the intraspecific agonistic display repertoire. Thompson suggested that time lost to caudal swinging could contribute to the depression of feeding rates in the field below the maximum rates obtained in the laboratory. With X. zealandica there was no discernible depression of feeding rate when two larvae in the laboratory occupied the same stem and interacted repeatedly. Predatory attacks by X. zealandica took only a few minutes and were interspersed between agonistic interactions. Uttley found that mutual interference as larvae stared at each other reduced the time available

for predatory activity. In X. zealandica the significance of this loss of time is unclear in view of the sporadic nature of predatory episodes. Crowley developed a model for an ESS with depressed feeding rates based generally on assumptions about the avoidance of potential cannibalism. Heads postulated that suppression of movement in the presence of predators would interfere with perch selection for maximal foraging rates.

In X. zealandica, as in other coenagrionid larvae (Lawton et al 1980, Thompson 1982), survival is largely decoupled from predatory success once a (low) threshold value is achieved. This is to be expected as any predator competent enough to cope with the hard times inherent in a stochastic environment will be grossly overequipped under normal or good conditions.

X. zealandica does not fulfil Pyke's first assumption, that fitness is dependent on behaviour while foraging, because survival and growth are not sensitive to changes in foraging success. Hence any attempt to interpret X. zealandica's larval biology in an OFT format is doomed to failure. Extracting the foraging component then analysing the effects of other life-history traits as perturbations on the foraging component is in essence the same as attempting to extract a principal component from an uncorrelated data set. The mathematics can be done, but the numerical result is meaningless. One is effectively trying to track noise. OFT is an inappropriate framework for either investigating or (Heinrich 1983) categorising the biology of X. zealandica.

Whereas species found on continental areas are largely buffered against environmental change through the opportunity to disperse or move along gradients to suitable habitats elsewhere, species on isolated islands face additional constraints. Because of the ever present possibility (and in evolutionary time the certainty) that conditions may be exceptionally harsh throughout the entire range of the species there

will be strong selection for robust phenotypes; those which can withstand the vagaries of a stochastic environment. Species on temperate islands represent the progeny of animals which survived both ice ages and interglacial maxima in situ. Robustness is to be expected in members of island faunas for through time their ancestors must have survived rapid, stochastic changes in circumstances from which they could not escape in space. However, robustness implies that under most conditions the animal's performance will be suboptimal. Robust performances are a property of 'satisficers', not of 'optimisers'.

As a long term survivor on an isolated island system X. zealandica would be expected to be robust in terms of its responses to environmental changes. The wide range of habitats occupied by, and the life-history flexibility of, the species (Rowe in press) appear to confirm this expectation.

In the general absence of long term studies of individual insects it was necessary to investigate a wide range of properties of X. zealandica larvae in an attempt to build a picture of the animals' lives. Larvae were followed at an individual level as the individual is the level at which natural selection operates and this therefore is the appropriate level to investigate questions of adaptation and selection pressures. This approach was in contrast to the general practice of measuring the bulk parameters of insect populations.

In this study I attempted to establish how the behaviours of individual larvae determine the pattern of site usage by examining site selection, activity on sites, site maintenance and feeding.

All instars of X. zealandica exhibit sedentary, sit and wait, behaviour patterns. A variety of perch sites were offered. Any object projecting from the aquarium floor appeared attractive to larvae. Second instar larvae localised on small cardboard squares while later instars

utilised pieces of plastic. Larvae raised from the egg in small containers remained on small cardboard squares cemented to the otherwise bare container floors until they dwarfed their perches.

In contrast to the habitual use of perches exhibited by X. zealandica, larvae of Xanthocnemis sobrina did not localise on perches in the second instar (but did localise in all later instars). Ischnura aurora the other coenagrionid species tested, used perch sites but did not localise and remain on a site for any length of time. The lestid Austrolestes colenisonis occasionally roosted on perches during the night but did not use them as hunting sites, ranging instead about the floor of the aquarium. A corduliid species (Procordulia grayi) showed no propensity to use perch sites offered.

X. zealandica larval behaviour on sites was remarkably consistent over a range of potential perches and a variety of prey types. Larvae on stems tended to remain near the base of the stem and to face the aquarium floor; larvae on roots occurred near the ends and faced outwards. Limited data was obtained on the use of branches extending from stems; the pattern of branch occupation appeared more affected by branch diameter than by other variables. Larval use of facsimile water plants was similar to the behaviour observed on stems (which simulated reeds and grasses). There was evidence of a weak increase in activity during the hours of darkness but no sign of any diel variation in the usage of perches.

The durations of site occupation by second and final instar larvae fitted negative exponential distributions when analysed as a semi-log plot of (cumulative) frequency vs duration. This distribution is generated by a simple Poisson process. There remained however, some consistent structure on these semi-log plots (Figs 59-63) and, when raw frequencies were analysed, discrepancies from a simple negative exponential distribution were apparent. This structure is at present unexplained. Differences in the mean duration of occupation of different

site types were reflected in the slopes of the semi-log plots. While in final instar larvae duration of site occupation was related to site geometry, second instar larvae on a single substrate type generated a series of internally consistent plots which differed between experiments.

Moulting must be a time of extreme stress for larvae. Massive physiological changes occur as body volume doubles and, for a period of some hours, the larva's mobility and defensive capability are markedly reduced. Approximately 50% of X. zealandica larvae abandoned their stems within hours of moulting. This probably reflected an increase in nervous activity in response to the stresses of moulting. What was surprising was that the durations of stem occupations of animals which did not abandon their stems immediately on moulting followed a simple negative exponential distribution with a decay constant similar to that of long occupancy, non-moulting larvae. Again this is indicative of some underlying structure in the animals' site occupation behaviour.

Developmental processes precluded the acquisition of data sequences long enough to permit detailed examination of site use by individuals. Even for an animal in diapause, a single 20, 30 or 40 day site residence time occupied a significant portion of the interstadial, leaving little time for other occupations. In one (extreme) case a larva occupied a site for 82 consecutive days (Rowe 1980). The limited data from individual larvae were however, consistent with the results above, and the structure found appears to be a consequence of the behaviour patterns of each individual larva.

The use of sit and wait tactics by animals with a heavy 'engineering' investment in a site is explicable, at least at a superficial level, in terms of reaping the benefit of the investment in the position; although (Lucas 1985, Janetos 1982), this investment may be far less than would appear at first glance. In contrast, the situation of

potentially mobile animals with no investment in site modification and which utilise superabundant sites presents an enigma. For such animals the use of an active foraging behaviour would appear to have advantages through the production of an increased encounter rate with prey. When the sit and wait behaviour of X. zealandica is contrasted with the more active foraging behaviours of Ischnura aurora and Austrolestes colenisonis the number of adaptive explanations must be severely limited; the more so as X. zealandica forcefully defend their sites from conspecifics.

Territorial behaviour involving aggressive interactions with conspecifics, opponents of approximately equal mobility and combative ability, must be expected to involve risks and potential costs to fitness. The potential costs are apparent; the benefits which offset these costs need to be established. Traditionally, analysis of site benefits has concentrated on access to some 'consumable' resource such as mates or food; however no such resources appear to be involved with X. zealandica. As larval X. zealandica are not (directly) involved in mating activity and appear, generally, to be faced with a superabundant supply of potential prey; and as the prey have no aggregation behaviour about the sites used by X. zealandica some alternative explanation is required.

Site defence occurs in X. zealandica larvae from the earliest free living stage*. While fights sometimes occur, most conflicts are resolved during bouts of display behaviour. As larvae develop, the display repertoire and the frequency of use of displays within the repertoire changes. I consider that the display repertoire alters in keeping with the increasing sensory capabilities of older larvae.

* Since the production of Chapter 2 (now published - N.Z. J. Zool. 12: 1-15) the abdomen bend display [12] has been seen in 2nd instar larvae.

X. zealandica differed from the other coenagrionid larva I examined (Ischnura aurora) in its larger display repertoire and the transformation of attack movements to displays. In contrast to I. aurora, X. zealandica was sedentary throughout its larval life. As female X. zealandica lay large numbers of eggs within a small area (Rowe in press) there is a high probability of larvae interacting with siblings. The ritualisation of attack behaviours in X. zealandica may be associated with a high level of relatedness among larvae in any area.

Andersson's (1980) argument on the plethora of threat displays is based on the premise that once encased in a velvet glove the mailed fist withers away. Threat displays generally differ from attack behaviours in the combination and amplitude of specific motor patterns. However, the primitive combinations underlying the ritualised behaviour are unlikely to have vanished. Any tendency for the mailed fist to atrophy and for 'bluff' displays (threat without either the inclination or the wherewithall to attack) to gain an ascendancy would produce an immediate selective advantage to any 'throw back' in which the thresholds for eliciting the primitive motor pattern were lower than the thresholds for the ritualised combinations.

As discussed in Chapter 2, I consider that ritualised threat displays are an ancillary activity undertaken while the displaying animal is attempting to evaluate its opponent. Displaying animals tread the tightrope of brinkmanship; like a lion-tamer they press their opponent, but they cannot risk pressing their opponent too far until they have ascertained that the asymmetries in the contest are significantly in their own favour. In this interpretation the fixed nature of displays has selective advantage as eccentric activity may inadvertently elevate the contest through the thresholds that release the primitive attack behaviour patterns of the opponent. Independent of any propensity of displays to transmit information on intention or RHP, the existence of a

multitude of threat displays permit displaying animals to disrupt their opponent's evaluation process. An animal switching displays presents its opponent with a new problem, perhaps with more or different information but, in a risk averse situation, producing a need for further analysis and buying time for the switcher to complete its own evaluation of the contest. While displaying, animals are involved in an information, disinformation, misinformation contest; communication occurs, but it is non-cooperative communication.

A consequence of my interpretation is that the number of displays in territorial species using the same signalling channels should (within reason) be independent of phylogeny. The size of the display repertoire should be determined by the underlying structures of conflict which determine the form of agonistic interactions at all levels, from dragonfly larvae to superpowers (Zeeman 1976). This appears to be born out (Table 4). At first sight the size of X. zealandica's display repertoire may appear inappropriate for a 'lowly invertebrate' but (as considered Chapter 2, Appendix 2) the ability of euryphagous insect predators to recognise potential prey may provide powerful preadaptations for discriminating between displays. The display repertoire sizes found would, in all probability, represent only a small fraction of the pattern recognition capability required for survival in a complex and chaotic habitat.

A further consequence of my interpretation is that the weaker animal (and probable loser) is more likely to initiate changes in displays (e.g. Clutton - Brock et al 1982). The analysis of conflict is however, still at a rudimentary stage (Rowe & Harvey 1985) and there is little data available. Because of the short length of sequences available for analysis and the distortions introduced by the non-cooperative nature of the exchange, crypt-analytic or deciphering techniques may prove more productive than the methods of communication engineering for analysing

animal signalling sequences. Traditional communication engineering methods presuppose that signaller and recipient are cooperating to transmit the message. In a non-cooperative system the absence of response due to a failure to receive and that due to a refusal to react or to a postponement of reaction will be indistinguishable; hence estimates of information transfer will be conservative.

Both recipients and displayers have coevolved with the displays. As an ability to evaluate the significance of displays accurately would be of selective advantage to recipients and as consistent (strong) intraspecific selection pressures would be acting throughout the evolution of the displays, appropriate 'discounting' capabilities can be expected to have evolved. Any tendency to inflate aggressive displays to manipulate recipients can be countered by the appearance of an appropriate level of 'cynicism'. Aggressive displays are unlikely to suffer from hyperinflation brought about by directional selection.

Under traditional analysis of agonistic displays as communication devices it has long been recognised that there are strong theoretical grounds for believing there is no selective advantage for displays which transmit information about intention (except the intention to depart) (Maynard Smith 1974, 1982). This has produced disagreements with field ethologists (van Rhijn 1980) and others (Enquist 1985) who argue that (reliable) information is transmitted during contests. Under my interpretation while there is no direct selection pressure for truth in advertising, hyperbole should be matched by cynicism and the consequences of involvement in escalated contests. Participants (and external observers) can obtain information by perception of changes in the displays used.

Why did my previous offering on X. zealandica's larval territoriality (Rowe 1980) fall on stony ground (Baker 1981a)? While differences in motor patterns, repertoire size and intensity of agonistic

behaviours do occur between species (Chapter 2, Harvey 1985) I suspect that the failure to confirm my findings on the occurrence of territorial behaviour was due largely to a failure of observers to watch animals closely; probably because the findings were outside their expectation. When I first drew the attention of P.S. Corbet to the displays and territorial behaviour of X. zealandica he was sceptical. However, after seeing the system in an aquarium he was convinced (Corbet 1980) and later his student Harvey (1985) detected similar behaviours in Pyrrhosoma nymphula.

X. zealandica larvae are sit and wait predators spending almost all their time on perches. During this investigation the duration of perch occupation followed an approximately negative exponential distribution with mean durations of site use up to 4-5 days on some sites and maximal durations commonly over 40 days (the recorded maximum was 82 days). Because of an absence of active search behaviour, sit and wait predators are random foragers (Hassell & Southwood 1978). Casual observation showed that for the later instars of X. zealandica the prey detection range was much greater than the attack range; therefore differential detectability of prey would have little effect on X. zealandica's predatory success. Glasser's (1984) challenge to the concept of 'random' foraging is not applicable to X. zealandica.

Whereas predatory versatility could be demonstrated relatively easily in Hemianax papuensis (Appendix 2) the cryptic behaviours of X. zealandica made investigations of predatory behaviour difficult. None-the-less, X. zealandica second instar larvae were found to have qualitatively and quantitatively different behaviour patterns with different prey types and in addition to more typical predatory behaviour late instar larvae scavenged large carcasses from the aquarium floor. X. zealandica larvae appeared to be competent and flexible predators which had little difficulty in attacking a wide range of prey types

successfully. It was noted that individual larvae varied in their usage of scavenging and, presumably, this would apply to other predatory tactics in a similar fashion to that found in H. papuensis.

There remains the question of why X. zealandica is an archetypal sit and wait predator, which defends its site from conspecifics, when other zygopteran larvae occurring in many of the same habitats (Ischnura aurora, Austrolestes colenisonis) adopt a more active foraging behaviour. It would seem the species must have evolved under markedly different environmental pressures. A possible explanation is that the other two species have sub-tropical origins (Rowe in press) in contrast to X. zealandica which is adapted to a (cool) temperate climate. While both I. aurora and A. colenisonis have the capability of being multivoltine, X. zealandica, like many (cool) temperate species, has a life-history pattern spanning an integral number of years. As discussed (p209) this life-history pattern generates a dichotomy of stable strategies. Fast developing species can absorb the effects of a high daily loss rate as they race to the reproductive stage; in contrast slow developing species need to maintain a very low daily loss rate to survive to the reproductive stage. Fast and slow development are different 'solutions' to imposed environmental constraints. Within the temperate zone, both solutions appear to coexist, perhaps with some help from a variable environment. The slow development pattern places a premium on loss reduction. Cryptic sit and wait tactics would tend to reduce losses to potential predators and at the same time to make the perch sites occupied valuable as refuges from predators. Thus sit and wait predation can be seen as a preadaptation to refuge defence territoriality.

In my view, predator avoidance dominates the larval life strategy of X. zealandica and foraging could be interpreted as a perturbation which interferes with the predator avoidance behaviour.

Site occupation and predatory behaviours of X. zealandica larvae displayed broad general patterns but on occasions wide individual variation was apparent. Variability in individual behaviours is a notorious problem in ecological studies; selection acts at level of the individual and therefore variability within and among individuals is a real property which must not be ignored. It is not an inconvenient aberration to be glossed over by taking the means of large samples. As in chemistry where coherence and insight came not from the detailed analysis of the bulk parameters of classical thermodynamics but through the consideration of the interactions of individual molecules, much biological enlightenment lies in understanding the seemingly erratic actions of the individual.

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REFERENCES

- Akre, B.G., Johnson, D.M., 1979: Switching and sigmoid functional response curves by damselfly naiads with alternative prey available. *J. Anim. Ecol.* 48: 703-720.
- Allbrook, P., 1979: Tasmanian Odonata. Fauna of Tasmania handbook No. 1. Hobart, University of Tasmania.
- Andersson, M., 1980: Why are there so many threat displays? *Journal of theoretical Biology* 86: 773-781.
- Ando, H., 1957: A comparative study on the development of ommatidia in Odonata. *Sci. Rep. Tokyo Kyoiku Daig. (B)* 8: 174-216.
- Andrew, R.J., 1983: Attention and information storage. *Abstr. 10th Int. Ethol. Conf.*: 10.
- Andrews, R.M., 1979: The lizard Corytophanes cristatus: an extreme "sit and wait" predator. *Biotropica* 11: 136-139.
- Armstrong, E.A., 1973: A study of bird song. New York, Dover Publications Inc. 343pp.
- Armstrong, J.S., 1958a: Notes on the occurrence of *Hemianax papuensis* (Burm.) in New Zealand. *Transactions of the Royal Society of New Zealand* 85: 713-714.
- Armstrong, J.S., 1958b: Notes on Ischnura aurora (Brauer), Odonata. *New Zealand entomologist* 2(2): 2-3.
- Armstrong, J.S., 1975/1980: original MS, edited as Armstrong, J.S., Corbet, P.S., 1980: Conversations about New Zealand dragonflies. Utrecht, Societas Internationalis Odonatologica Rapid Communications 2, 73pp.
- Asahina, S., 1950: On the life-history of Epiophlebia superstes (Odonata, Anisozygoptera). *Proceedings of the VIIIth International Congress of Entomology*. Stockholm: 337-341.

- Aspey, W.P., 1977: Wolf spider sociobiology: I. Agonistic display and dominance-subordinance relations in adult male *Schizocosa crassipes*. *Behaviour* 62: 103-141.
- Baker, R.L., 1980: Use of space in relation to feeding areas by zygopteran nymphs in captivity. *Canadian Journal of Zoology* 58: 1060-1065.
- Baker, R.L., 1981a: Behavioural interactions and the use of feeding areas by nymphs of Coenagrion resolutum (Coenagrionidae: Odonata). *Oecologia* 49: 353-358.
- Baker, R.L., 1981b: Use of space in relation to areas of food concentration by nymphs of Lestes disjunctus (Lestidae: Odonata) in captivity. *Canadian Journal of Zoology* 59: 134-135.
- Baker, R.L., 1982: Effects of food abundance on growth, survival, and use of space by nymphs of *Coenagrion resolutum* (Zygoptera). *Oikos* 38: 47-51.
- Baker, R.L., 1983: Spacing behaviour by larval Ischnura cervula Selys: effects of hunger, previous interactions and familiarity with an area (Zygoptera: Coenagrionidae). *Odonatologica* 12: 201-207.
- Baker, R.L., Clifford, H.F., 1981: Life cycles and food of Coenagrion resolutum (Coenagrionidae: Odonata) and Lestes disjunctus disjunctus (Lestidae: Odonata) populations from the boreal forest of Alberta Canada. *Aquatic insects* 3: 179-191.
- Baker, R.R., 1983: Insect territoriality. *Ann. Rev. Ent.* 28: 65-89.
- Baldus, K., 1924: Experimentale Untersuchungen über die Entfernungslokalisation der Libellen (Aeschna cyanea). *Z. vergl. Physiol.* 3: 475-505.

- Barlow, G.W., 1977: Modal action patterns. in T.A. Sebeok [ed] How animals communicate. Bloomington, Indiana University Press pp98-134.
- Bay, E.C., 1974: Predator-prey relationships among aquatic insects. Annual Review of Entomology 19: 441-453.
- Bell, W.J., Gorton, R.E., 1978: Informational analysis of agonistic behaviour and dominance hierachy formation in a cockroach *Nauphoeta cinerea*. Behaviour 67: 217-235.
- Benke, A.C., Benke, S.S., 1975: Comparative dynamics and life histories of coexisting dragonfly populations. Ecology 56: 302-317.
- Benke, A.C., Crowley, P.H., Johnson, D.M., 1982: Interactions among coexisting larval Odonata: an in situ experiment using small enclosures. Hydrobiologia 94: 121-130.
- Berenbaum, M.R., Miliczky, E., 1984: Mantids and milkweed bugs: efficacy of aposematic coloration against invertebrate predators. American Midland Naturalist 111: 64-68.
- Bergerud, A.T., 1983: Prey switching in a simple ecosystem. Sci. Am. 249(6): 116-124.
- Billingsley, P., 1961: Statistical inference for Markov processes. Chicago, U. Chicago Press 75pp.
- Black, R., 1971: Hatching success in the three-spined stickleback, Gasterosteus aculeatus, in relation to changes in behaviour during the parental phase. Anim. Behav. 19: 532-541.
- Blair, D., Finlayson, C.M., 1981: Observations on the habitat and biology of a lymnaeid snail, Austropeplea vinosa (Gastropoda: Pulmonata), an intermediate host for avian schistosomes in tropical Australia. Australian Journal of Marine and Freshwater Research 32: 757-767.

- Boake, C.R.B., Andow, D., Visscher, P.K., 1984: Spacing of ant-lions and their pits. *Am. Midl. Nat.* 111: 192-194.
- Caillere, L., 1965: Description du reflexe de capture chez la larve d'*Agrion splendens* Harris 1782 (Insecte, Odonate, Zygoptere). *Bulletin Mensuel Societe Linneenne Lyon* 34(10): 424-434.
- Caillere, L., 1972: Dynamics of the strike in *Agrion* (syn, *Calopteryx*) *splendens* Harris 1782 larvae (Odonata: Calopterygidae). *Odonatologica* 1: 11-19.
- Caillere, L., 1973: Comportement de capture chez la larve d'*Agrion splendens* Harris (Odonopteres): comparaison entre la larve agee et la larve du premier stade. *Rev. Comp. an. Fr.* 7: 289-312.
- Caillere, L., 1974: Ontogenese du comportement de capture chez la larve d'*Agrion* (*Calopteryx* auct.) *splendens* Harris (Odonopteres). *Behaviour* 51(3-4): 166-194.
- Carlin, N.E., Johnston, A.B., 1984: Learned enemy specification in the defense recruitment system of an ant. *Naturwissenschaften* 71: 156-157.
- Carpenter, F.M., 1977: Geological history and the evolution of the insects. *Proceedings of the 15th International Congress of Entomology, Washington D.C.* : 63-70.
- Chutter F.M., 1961: Certain aspects of the morphology and ecology of the nymphs of several species of *Pseudagrion* Selys (Odonata). *Arch. Hydrobiol.* 57: 430-463.
- Cloarec, A., 1972: Revue generale de comportements alimentaires d'insectes predateurs et leur regulation. *Annee Biol.* 11(5-6): 257-290.

- Cloarec, A., 1975: Variations quantitatives circadiennes de la prise alimentaire des larves d'Anax imperator Leach (Anisoptera: Aeshnidae). *Odonatologica* 4: 137-147.
- Cloarec, A., 1976: Interactions between different receptors involved in prey capture in Ranatra linearis (Insect, Heteroptera). *Biology of Behaviour* 1: 251-266.
- Clutton-Brock, T.H., Guinness, F.E., Albon, S.D., 1982: Red deer: behavior and ecology of two sexes. Chicago, U. of Chicago Press.
- Conover, W.J., 1980: Practical nonparametric statistics. N.Y. John Wiley 493pp.
- Corbet, P.S., 1952: An adult population study of Pyrrhosoma nymphula (Sulzer) (Odonata: Coenagrionidae). *Journal of Animal Ecology* 21: 206-222.
- Corbet, P.S., 1953: A terminology for the labium of larval Odonata. *The Entomologist* 86: 191-196.
- Corbet, P.S., 1955: The larval stages of the emperor dragonfly, Anax imperator Leach (Odonata: Aeshnidae). *Entomological Gazette, London* 6: 189-204.
- Corbet, P.S., 1957a: The life-histories of two summer species of dragonfly (Odonata: Coenagriidae). *Proc. Zool. Soc. London* 128: 403-418.
- Corbet, P.S., 1957b: The life-history of the Emperor Dragonfly Anax imperator Leach (Odonata: Aeshnidae). *J. Anim. Ecol.* 26: 1-69.
- Corbet, P.S., 1960: in Corbet, P.S., Longfield, C., Moore, N.M., *Dragonflies*. London, Collins 260pp.
- Corbet, P.S., 1962: *A biology of dragonflies*. London, Witherby 247pp.
- Corbet, P.S., 1980: Biology of Odonata. *Annual Review of Entomology* 25: 189-217.

- Corbet, P.S., Scrimgeour, C.M., Holmquist, J.E., Kiauta, B., 1984: A topic index for Odonatological abstracts 1-4225 from Odonatologica volumes 1-12. Utrecht, Societas Internationalis Odonatologica Rapid Communications (suppl.) 4B, VIII + 52pp.
- Crowley, P.H., 1979: The behavior of zygopteran nymphs in a simulated weed bed. Odonatologica 8: 91-101.
- Crowley, P.H., 1984: Evolutionary stable strategies for larval dragonflies. Lecture notes in biomathematics 54: 55-74. Berlin, Springer Verlag.
- Crumpton, W.J., 1979: Aspects of the biology of Xanthocnemis zealandica and Austrolestes colenisonis at three ponds in the South Island, New Zealand. New Zealand Journal of Zoology 6: 285-297.
- Curio, E., 1976: The ethology of predation. New York, Springer-Verlag. 250pp.
- Daellenbach, H.G., George, J.A., McNickle, D.C., 1983: Introduction to operations research techniques, second edition. Boston, Allyn & Bacon 711pp.
- Darwin, C., 1872: The expression of the emotions in Man and Animals. London, J. Murray 374pp.
- Davies, D.A.L., 1981: Synopsis of the extant genera of the Odonata. Utrecht, Societas Internationalis Odonatologica Rapid Communications 3, 59pp.
- Davies, N.B., 1978: Ecological questions about territorial behaviour in Krebs, J.R., Davies, N.B. [eds] Behavioural ecology an evolutionary approach. Oxford, Blackwood Scientific Publications: 317-350.

- Davies, N.B., Houston, A.I., 1981: Owners and satellites: the economics of territory defence in the pied wagtail Motacilla alba. J. Anim. Ecol. 50: 157-180.
- Davis, E.D., 1974: Behavior as an ecological factor. Benchmark papers in ecology. Stroudsburg Pa, Dowden, Hutchinson & Ross Inc. xv+390pp.
- Deacon, K.J., 1979: The seasonality of four Odonata species from mid Canterbury, South Island, New Zealand. Unpubl. PhD thesis, University of Canterbury, Christchurch 209pp.
- Donnelly, T.W., 1974: Odonata collecting "Down Under". Selysia 6(2): 1-7.
- Donnelly, T.W., 1984: Melanesobasis gen. nov., a new genus of Fijian damselflies: a possible link between the platycnemidid Lieftinckia and certain coenagrionids (Zygoptera). Odonatologica 13: 89-105.
- Dow M., Ewing A.W., Sutherland, I., 1976: Studies of the behaviour of cyprinodont fish III. The temporal patterning of aggression in Aphysemion striatum (Boulenger). Behaviour 59: 252-268.
- Dowdle W., 1981: Feeding ecology of predatory insects in Remus pond, Cass. Unpubl. B.Sc.(hons) proj. Dept. Zoology U. of Canterbury 95pp.
- Dumbleton, L.J., 1970: The present status of taxonomic entomology in New Zealand. Aquatic orders and Neuroptera. New Zealand Entomologist 4(3): 38-40.
- Eibl-Eibesfeldt, I., 1970: Ethology; the biology of behavior [E. Klinghammer transl.] New York, Holt, Rinehart and Winston 530 pp.
- Enquist, M., 1985: Communication during aggressive interactions with particular reference to variation in choice of behaviour. Anim. Behav. 33: 1152-1161.

- Evans, M.E.G., 1985: Aspects of insects (review of Evans, H.E. 198 .
Insect biology: a textbook of entomology). Nature 314: 32.
- Fagen, R.M., Young, D.Y., 1978: Temporal patterns of behaviors:
durations, intervals, latencies and sequences. In Colgan,
P.W., [ed] Quantitative ethology. N.Y., Wiley 364pp.
- Fitzpatrick, S.M., Wellington, W.G., 1983: Insect territoriality. Can. J.
Zool. 61: 471-486.
- Folsom, T.C., Collins, N.C., 1984: The diet and foraging behavior of the
larval dragonfly *Anax junius* (Aeshnidae), with an
assessment of the role of refuges and prey activity. Oikos
42: 105-113.
- Formanowicz, D.R., Bobka, M.S., Brodie, E.D., 1982: The effects of prey
density on ambush-site changes in an extreme ambush-type
predator. Am. Middl. Nat. 108: 250-255.
- Fraser, F.C., 1927: Odonata. in Buxton P.A. [ed] Insects of Samoa and
other terrestrial arthropoda. Bulletin of the British
Museum (Natural History) 7(1): 19-44.
- Fraser, F.C., 1953: Further notes on Samoan Odonata belonging to the
Ischnurine complex of species, with descriptions of two new
species and some unknown females. Proceedings of the Royal
Entomological Society London (B) 22: 119-126
- Fraser, F.C., 1957: A reclassification of the order Odonata. Sydney,
Royal Zoological Society of New South Wales 133pp.
- Freed, A.N., 1984: Foraging behaviour in the jumping spider Phidippus
audax: bases for selectivity. Journal of Zoology London
203: 49-61.
- Fremlin, J., 1979: Dinosaur death: the unconsciousness factor. New
Scientist 81: 250-251.
- Gardner, A.E., 1951: The early stages of Odonata. Proc. S. London Ent.
and Nat. Hist. Soc. 1950-51: 83-88.

- Gardner, A.E., 1956: The biology of dragonflies. Proceedings of the South London entomological and natural history Society 1954-5: 109-134.
- Gaufin, A.R., Clubb, R., Newell, R. 1974: Studies on the tolerance of aquatic insects to low oxygen concentrations. Great Basin Naturalist 34(1): 45-59.
- Gibbs, G.W., 1980: New Zealand butterflies identification and natural history. Auckland, Collins 207pp.
- Giller, P.S., 1982: Locomotory efficiency in the predation strategies of the British Notonecta (Hemiptera: Heteroptera). Oecologia 52: 273-277.
- Gilpin, M.E., 1974: Habitat selection and a Liapunov function for competition communities. [in] Lecture notes in Biomathematics 2: 62-65. Berlin, Springer-Verlag.
- Glasser, J.W., 1979: The role of predation in shaping and maintaining the structure of communities. Am. Nat. 1113: 631-641.
- Glasser, J.W., 1984: Is conventional foraging theory optimal? Am. Nat. 124: 900-905.
- Greenstone, M.H., 1983: Site-specificity and site tenacity in a wolf spider: a serological dietary analysis. Oecologia 56: 79-83.
- Griffiths, D., 1973: The food of animals in an acid moorland pond. J. Anim. Ecol. 42: 285-293.
- Griffiths, D., 1981: Sub-optimal foraging in the ant-lion Macroleon quinquemaculatus. J. Anim. Ecol. 50: 697-702.
- Griffiths, D., 1982: Tests of alternative models of prey consumption by predators, using ant lion larvae. J. Anim. Ecol. 52: 363-373.

- Grossman, G.D., 1980: Food, fights, and burrows: the adaptive significance of intraspecific aggression in the bay goby (Pisces: Gobiidae). *Oecologia* 45: 261-266.
- Hailman, J.P., 1977: Communication by reflected light in T.A. Sebeok [ed] How animals communicate. Bloomington, Indiana University Press pp184-210.
- Harnisch, O. 1958. Untersuchungen an den Analkiemern der Larve von Agrion. *Biol. Zbl.* 77: 300-310.
- Harvey, I.F., 1985: Larval spacing behaviour of two species of dragonfly (Odonata: Zygoptera). Unpubl. PhD. thesis U. of Dundee.
- Hassell, M.P., Southwood, T.R.E., 1978: Foraging strategies of insects. *Annual Review of Ecology and Systematics* 9: 75-98.
- Hazlett, B.A., Estabrook, G.F., 1974: Examination of agonistic behavior by character analysis: Hermit crabs. *Behaviour* 49: 88-110.
- Heads, P.A., 1985: The effect of invertebrate and vertebrate predators on the foraging movements of Ischnura elegans larvae (Odonata: Zygoptera). *Freshwater Biology* 15: 559-571.
- Heinrich, B., Heinrich, M.J.E., 1984: The pit-trapping foraging strategy of the ant lion, Myrmeleon immaculatus DeGeer (Neuroptera: Myrmeleontidae). *Behav. Ecol. Sociobiol.* 14: 151-160.
- Heinrich, H., 1983: Do bumblebees forage optimally and does it matter. *Am. Zool.* 23: 273-281.
- Heinroth, O., 1911: Beitrage zur Biologie, namentlich Ethologie und Psychologie der Anatiden. *Verh. V Int. Orn. Kongr., Berlin* 589-702.
- Heymer, A., 1970: Die funktion der kaudalstacheln bei Aeschna-larven beim beutefang-und aggressionsverhalten [Odon. Anisoptera] mit einer Diskussion uber den Farbensinn und die Gestaltspertzption. *Ann. Soc. ent. Fr. (N.S.)* 6: 637-645.

- Heymer, A., 1973: Verhaltensstudien an Prachtlibellen. Beitrage zur Ethologie und Evolution der Calopterygidae Selys, 1850 (Odonata; Zygoptera). Z. fur Tierpsychol. suppl. 11: 1-100.
- Hinde, R.A., 1956: The biological significance of the territories of birds. Ibis 98: 340-369.
- Holling, C.S., 1966: The functional response of invertebrate predators to prey density. Mem. Ent. Soc. Canada 48: 1-86.
- Horridge, G.A., 1978: The separation of visual axes in apposition compound eyes. Philosophical transactions of the Royal Society London series B 285, 1003: 1-59.
- Hudson, G.V., 1904: New Zealand Neuroptera. London, West, Newman. 102pp + 11pl.
- Huey, R.B., Pianka, E.R., 1981: Ecological consequences of foraging mode. Ecology 62: 991-999.
- Hurlbert, S.H., 1984: Pseudoreplication and the design of ecological field experiments. Ecol. Monogr. 54: 187-211.
- Hutchinson, G.E., 1959: Homage to Santa Rosalia or why are there so many kinds of animals? Am. Nat. 80: 440-457.
- Hutchinson, R., 1976: Les protozoaires dans l'alimentation des jeunes larvæ des libellules. Cordulia 2: 152-155.
- Hutton, F.W., 1898: On a collection of insects from the Chatham Islands with descriptions of three new species. Transactions and Proceedings of the New Zealand Institute 30: 155-160.
- Hutton, F.W., 1899: The Neuroptera of New Zealand. Transactions of the New Zealand Institute 31: 208-249.
- Hyatt, G.W., Salmon, M., 1978: Combat in the fiddler crabs *Uca pugilator* and *U. pugnax*: a quantitative analysis. Behaviour 65: 182-211.

- Inoue, T., Matsura, T., 1983: Foraging strategy of a mantid Paratenodera angustipennis S.: mechanism of switching tactics between ambush and active search. *Oecologia* 56: 264-271.
- Jachowski, R.L., 1974: Agonistic behavior of the blue crab, Callinectes sapidus Rathbun. *Behaviour* 50: 232-253.
- Jackson, R.R., Blest, A.D., 1982: The biology of Portia fimbriata, a web building jumping spider (Araneae, Salticidae) from Queensland: utilization of webs and predatory versatility. *Journal of zoology London* 196: 255-293.
- Jackson, R.R., Harding, D.P., 1982: Intraspecific interactions of Holoplatys sp. indet. a New Zealand jumping spider (Araneae: Salticidae). *New Zealand journal of zoology* 9: 487-510.
- Jackson, R.R., Pollard, S.D., 1982: The biology of Dysdera crocata (Araneae: Dysderidae): intraspecific interactions. *Journal of zoology (London)* 198: 197-214.
- Janetos, A.C., 1982: Foraging tactics of two guilds of web-spinning spiders. *Behav. Ecol. Sociobiol.* 10: 19-27.
- Jansson, A., Vuoristo, T., 1979: Significance of stridulation in larval Hydropsychidae (Trichoptera). *Behaviour* 71: 167-186.
- Janzen, D.H., 1977: Why fruits rot, seeds mold and meat spoils. *Am. Nat.* 111: 691-713.
- Jarzembowski, E.A., 1984: Early Cretaceous insects from southern England. *Modern Geology* 9: 71-93.
- Jellyman, D.J., 1979: Observations on the biology of the giant kokopu, Galaxius argenteus (Gmelin 1789). *Mauri Ora* 7: 53-61.
- Jensen, A.L., 1980: The karyotype of five species of Odonata endemic to New Zealand. *Odonatologica* 9: 29-33.

- Johannsson, O. E., 1978: Co-existence of larval Zygoptera (Odonata) common to the Norfolk Broads (U.K.) I. Temporal and spatial separation. *Oecologia* (Berl.) 32: 303-321.
- Johnson, C., 1975: Polymorphism and natural selection in ischnuran damselflies. *Evol. theory* 1: 81-90.
- Johnson, D.M., 1973: Predation by damselfly naiads on cladoceran populations: fluctuating intensity. *Ecology* 54: 251-268.
- Johnson, D.M., Akre, B.G., Crowley, P.H., 1975: Modeling arthropod predation: wasteful killing by damselfly naiads. *Ecology* 56: 1081-1093.
- Johnson, D.M., Bohanan, R.E., Watson, C.N., Martin, T.H., 1984: Coexistence of Enallagma divagens and Enallagma traviatum in Bays Mountain Lake, Tennessee: an in situ enclosure experiment. *Adv. Odonatol.* 2: 57-70.
- Johnson, D.M., Crowley, P.H., 1980: Odonate "hide and seek": Habitat-specific rules? in Kerfoot, W.E. [ed] *Evolution and ecology of zooplankton communities*. Spec. Symp. Vol. 3, Amer. Soc. Limnol. Oceanogr. Hanover NH. University Press of New England pp 569-579.
- Kacelnik, A., Houston, A.I., Krebs, J.R., 1981: Optimal foraging and territorial defence in the Great Tit (Parus major). *Behav. Ecol. Sociobiol.* 8: 35-40.
- Kaufman, J.H. 1983: On the definitions and functions of dominance and territoriality. *Biol. Rev.* 58: 1-20.
- Keetch, D.P., Moran, V.C., 1966: Observation on the biology of nymphs of Paragomphus cognatus. Habitat selection in relation to substrate particle size. *Proc. R. Ent. Soc. Lond.* A41(7-9): 116-122.

- Kime, J.B., 1974: Ecological relationships among three species of aeshnid dragonfly larvae. unpubl. PhD. thesis University of Washington. 142pp.
- Kimmins, D.E., 1970. A list of the type-specimens of Odonata in the British Museum (Natural History) part III. Bulletin of the British Museum (Natural History) 24(6): 171-205.
- Klekowski, R.Z., Kamler, E., 1968: Flowing-water polarographic respirometer for aquatic animals. Polskie Arch. Hydrobiol. 15: 121-144
- Knisley, C.B., Pearson, D.L., 1981: The function of turret building behaviour in the larval tiger-beetle Cicindela willistoni (Coleoptera: Cicindelidae). Ecol. Ent. 6: 401-410.
- Krebs, J.R., 1971: Territory and breeding density in the great tit, Parus major L. Ecology 52: 2-22.
- Krebs, J.R., Davies, N.B., 1978: Behavioural ecology: an evolutionary approach. Oxford, Blackwell Scientific Publications Ltd. 506pp.
- Krebs, J.R., Davies, N.B., 1984: Behavioural ecology: an evolutionary approach. 2nd edition. Oxford, Blackwell Scientific Publications Ltd.
- Krebs, J.R., Stephens, D.W., Sutherland, W.J., 1983: Perspectives in optimal foraging. [in] Perspectives in Ornithology. Cambridge U.P. pp165-215.
- Lambert, D.M., Paterson, H.E., 1982: Morphological resemblance and its relationship to genetic distance measures. Evolutionary Theory 5: 291-300.
- Lawton, J.H., 1970a: A population study on larvae of the damselfly Pyrrhosoma nymphula (Sulzer) (Odonata: Zygoptera). Hydrobiologia 36: 33-52.

- Lawton, J.H., 1970b: Feeding and food energy assimilation in larvae of the damselfly Pyrrhosoma nymphula (Sulz.) (Odonata: Zygoptera). *Journal of Animal Ecology* 39: 669-689.
- Lawton, J.H., 1971a: Ecological energetics studies in larvae of the damselfly Pyrrhosoma nymphula (Sulzer). *Journal of Animal Ecology* 40: 385-423.
- Lawton, J.H., 1971b: Maximum and actual feeding-rates in larvae of the damselfly Pyrrhosoma nymphula (Sulzer) (Odonata: Zygoptera). *Freshwater Biology* 1: 99-111.
- Lawton, J.H., Beddington, J.R., Bonser, R., 1974: Switching in invertebrate predators. *in* Usher, M.B., and Williamson, M.H. [eds] *Ecological stability*. London, Chapman and Hall Ltd. pp 141-158.
- Lawton, J.H., Thompson, B.A., Thompson D.J., 1980: The effect of prey density on survival and growth of damselfly larvae. *Ecological Entomology* 5: 39-51.
- Lee, C.L., Fielder, D.R., 1983: Agonistic behaviour and the development of dominance hierarchies in the freshwater prawn Macrobrachium australiense Holthius, 1950 (Crustacea: Palaemonidae). *Behaviour* 83: 1-17.
- Lieftinck, M.A., 1940: Revisional notes on some species of Copera Kirby. With notes on habits and larvae (Odon., Platycneminidae). *Treubia* 17: 281-306.
- Lieftinck, M.A., 1975: The dragonflies (Odonata) of New Caledonia and the Loyalty Islands. *Cah. O.R.S.T.O.M. serie Hydrobiol.* IX(3): 127-166.
- Lorenz, K., 1941: Vergleichende Bewegungsstudien an Anatinen. *J. Orn.* 89 (suppl.): 194-294.
- Lorenz, K.Z., 1967: (M. Latzke [trans.]) *On aggression*. London, Methuen. 273pp.

- Lorenz, K., 1981: The foundations of ethology. New York, Springer-Verlag.
379pp.
- Lucas, J.R., 1985: Metabolic rates and pit-construction costs of two antlion species. *J. Anim. Ecol.* 54: 295-309.
- Macan, T.T., 1964: The Odonata of a moorland fishpond. *Internationale Revue der Gesamten Hydrobiologie* 49: 325-360.
- Macan, T.T., 1965: The fauna of the vegetation of a moorland fishpond. *Arch. Hydrbiol.* 61: 273-310.
- Macan, T.T., 1977: The influence of predation on the composition of freshwater animal communities. *Biol. Rev.* 52: 45-70.
- Machado, A.G.M., 1977: Ecological studies on on the larva of the plant-breeding damselfly Roppaneura beckeri Santos 1966. *Abstr. 4th Int. Symp. Odonatol. Gainesville*: 11.
- McDowall, R.M., 1978: New Zealand freshwater fishes: a guide and natural history. Auckland, Hienemann Educational 230pp.
- McGlone, M.S., 1983: The history of the New Zealand lowland forest since the last glaciation. [in] *Lowland Forests in New Zealand*. Hamilton, University of Waikato. pp 1-16.
- McLachlan, R., 1873: A catalogue of the neuropterous insects of New Zealand; with notes and descriptions of new forms. *Ann. Mag. Nat. Hist.* 4(12): 30-42.
- McLachlan, R., 1894: Some additions to the neuropterous fauna of New Zealand. *Entomologist's Monthly Magazine* 30: 238-243, 270-272.
- MacKinnon, J., 1970: Indications of territoriality in mantid. *Z. Tierpsychol.* 27: 150-155.
- MacNeill, N., 1960: A study of the caudal gills of dragonfly larvae of the sub-order Zygoptera. *Proc. Roy. Irish Acad.* 61(B): 115-140 + 6 pl.

- Marler, P., 1977: The evolution of communication in T.A. Sebeok [ed]
How animals communicate. Bloomington, Indiana University
Press pp45-70.
- Martin, I.G., 1980: An ethogram of captive Blarina brevicauda. American
midland naturalist 104: 290-294.
- Martindale, S., 1982: Nest defense and central place foraging: a model
and experiment. Behav. Ecol. Sociobiol. 10: 85-90.
- Maynard Smith, J., 1974: The theory of games and the evolution of animal
conflicts. J. theor. Biol. 47: 209-221.
- Maynard Smith, J., 1982: Evolution and the theory of games. Cambridge,
Cambridge University Press 224pp.
- Miller, D., 1955: Native insects. Wellington, Reed. 65pp.
- Mori, A., Wada, Y., 1974: The hourly activity of the larvae of three
species of dragonflies feeding on mosquito larvae. Tropical
Medicine 16: 41-44.
- Moynihan, M., 1970: Control, Suppression, Decay, Disappearance and
Replacement of Displays. Journal of theoretical biology 29:
85-112.
- Myers, J.P., 1983: Commentary [on Krebs et al 1983] [in] Perspectives
in Ornithology. Cambridge U.P. pp216-221.
- Mylechreest, P., 1978: Some effects of a unique hydroelectric development
on the littoral benthic community and ecology of trout in a
large New Zealand lake. unpubl. M.Sc. thesis University of
British Columbia 103pp.
- O'Farrell, A.F., 1970: Odonata (Dragonflies and damselflies) in I.M.
MacKerras [ed] The insects of Australia. Carlton, Melbourne
University Press. pp241-261.
- Olive, C.W., 1982: Behavioral response of a sit-and-wait predator to
spatial variation in foraging gain. Ecology 63: 912-920.

- Paulian, R., Serfaty, A., 1944: Le rythme nycthemeral des larves d'Aeschnes. Bull. Mus. Hist. Nat. Paris 16: 442-447.
- Pearlstone, P.S.M., 1973: The food of damselfly larvae in Marion Lake, British Columbia. Syesis 6: 33-39.
- Pennak, R.W., McColl, C.M., 1944: An experimental study of oxygen absorption in some dragonfly naiads. J. cell. comp. Physiol. 23: 1-10.
- Penniket, J.G., 1966: Keys to the nymphs and adults of the New Zealand Odonata. Records of the Canterbury Museum 8(2): 87-92.
- Petr, T., 1968: Population changes in aquatic invertebrates living on two water plants in a tropical man-made lake. Hydrobiologia 32: 449-485.
- Phillips, R.R., Swears, S.B., 1979: Social hierachy, shelter use and avoidance of predacious toad fish (Opsanus tau) by the striped blenny (Chasmodes bosquianus). Anim. Behav. 27: 1113-1121.
- Pilon, J-G, Masseau, M.J., 1983: Morphologie externe des larves de Enallagma hageni (Walsh) (Zygoptera: Coenagrionidae). Odonatologica 12: 125-140.
- Popham, E.J., 1954: A new and simple method of demonstrating the physical gill of aquatic insects. Proc. R. ent. Soc. Lond. A29: 51-54.
- Pritchard, G., 1964: The prey of dragonfly larvae in ponds in northern Alberta. Canadian Journal of Zoology 42: 785-800.
- Pritchard, G., 1965a: Prey capture by dragonfly larvae. Canadian Journal of Zoology 43: 271-289.
- Pritchard, G., 1965b: Sense organs in the labrum of Aeshna interrupta lineata Walker (Odonata; Anisoptera). Canadian Journal of Zoology 43: 333-336.

- Prodon, R., 1976: Le substrat, facteur ecologique et ethologique de la vie aquatique. Dipl. Doct. Spec. Sci. Biol. thesis U. Claude Bernard Lyon 221pp.
- Pyke, G.H., 1984: Optimal foraging theory: a critical review. *Ann. Rev. Ecol. Syst.* 15: 523-575.
- Rease Nevin, F., 1929: A study of the larva of *Calopteryx* (Agrion) *maculata* (Odonata, Agrionidae). *Trans. Am. Ent. Soc.*
- Rechten, C., Fernald R.D., 1979: A sampled randomization test for examining single cells of behavioural transition matrices. *Behaviour* 79: 217-227.
- Richard, G., 1960: Les bases sensorielles du comportement de capture des proies par diverses larves d'odonates. *J. Psychol. norm. path.* 1: 95-107.
- Richard, G., 1961: Ontogenese du comportement chez diverses larves d'Odonates.
- Richard, G., 1962: Contributions a l'etude ethologique des odonates. *Proc. XIth Int. Congr. Ent. Vienna.* 11(1): 604-607.
- Riechert, S.E., 1978: Games spiders play: behavioral variability in territorial disputes. *Behav. Ecol. Sociobiol.* 3: 135-162.
- Rivard, D., Pilon, J.G., 1977: Etude de la variation intra-stade au cours du developpement larvaire de *Enallagma vernale* Gloyd (Zygoptera: Coenagrionidae): discussion sur le mecanisme de differentiation des types de developpement. *Odonatologica* 6: 181-198.
- Robert, P.A., 1958: Les libellules (odonates). Neuchatel, Delachaux et Niestle S.A.
- Robertson, H.M., Paterson, H.E.H., 1982: Mate recognition and mechanical isolation in Enallagma damselflies (Odonata: Coenagrionidae). *Evolution* 36: 243-250.

- Robinson, W.R., Peters, R.H., Zimmerman, J., 1983: The effects of body size and temperature on the metabolic rate of organisms. *Canadian Journal of Zoology* 61: 281-288.
- Rowe, G.W., Harvey, I.F., 1985: Information content in finite sequences: communication between dragonfly larvae. Applied analysis report. Dept. mathematical sciences, U. of Dundee (in press *J. theor. Biol.*)
- Rowe, R.J., 1978a: Some aspects of the behaviour of Xanthocnemis zealandica larvae. unpubl. proj. Dept Zoology U. of Canterbury 43pp.
- Rowe, R.J., 1978b: Ischnura aurora (Brauer), a dragonfly with unusual mating behaviour. *Odonatologica* 7: 375-383.
- Rowe, R.J., 1979: A method for marking aquatic insect larvae. *Mauri Ora* 7: 143-145.
- Rowe, R.J., 1980: Territorial behaviour of a larval dragonfly, Xanthocnemis zealandica (McLachlan) (Zygoptera: Coenagrionidae). *Odonatologica* 9: 285-292.
- Rowe, R.J., 1981: A new species of Xanthocnemis Tillyard (Odonata: Coenagrionidae) from the Chatham Islands, New Zealand. *Records of the Auckland Institute and Museum* 18: 205-209.
- Rowe, R.J. in press: The dragonflies of New Zealand. Auckland, Auckland University Press, Oxford University Press.
- Rypstra, A.L., 1982: Building a better insect trap: an experimental investigation of prey capture in a variety of spider webs. *Oecologia* 52: 31-36.
- Sandegren, F.E., 1976: Agonistic behavior in the male northern elephant seal. *Behaviour* 57: 136-158.
- Savan, B.I., 1979: Studies on the foraging behaviour of damselfly larvae (Odonata: Zygoptera). unpubl. PhD. thesis University of London 246+pp.

- Schoener, T., 1971: Theory of feeding strategies. *Ann. Rev. Ecol. Syst.* 2: 369-404.
- Scott, R.R., 1971: The larval instars of Xanthocnemis zealandica (Odonata: Coenagrionidae). *N.Z. Ent.* 5: 38-46.
- Selys-Longchamps, M.E. de, 1876: Synopsis des agrionines, 5me legion, Agrion. *Bull. Acad. R. Sci. Lettres Beaux-arts Belg.* (2) 41: 247-322; 496-539; 1233-1309 and (2) 42: 490-531; 952-991.
- Siegel, S., 1956: Nonparametric statistics for the behavioral sciences. Tokyo, McGraw-Hill Kogakusha. 312pp.
- Simon, H.A., 1956: Rational choice and the structure of the environment. *Psychol Reviews* 63: 129-138.
- Sokal, R.R., Rohlf, F.J., 1981: Biometry. N.Y., Freeman. 859pp
- Southwood, T.R.E., 1978: The components of diversity. *Symp. R. ent. Soc. Lond.* 9: 19-40.
- Stamps, J., 1983: Territoriality and the defence of predator-refuges in juvenile lizards. *Anim. Behav.* 31: 857-870.
- Staples, D.J., 1975: Production biology of the upland bully Philypnodon breviceps Stokell in a small New Zealand lake. *J. Fish Biol.* 7: 1-24.
- Stark, J.D., 1981: Trophic relationships, life-histories and taxonomy of some invertebrates associated with aquatic macrophytes in Lake Grasmere. unpubl. PhD. thesis University of Canterbury, Christchurch. 256pp.
- Stevens, G.R., 1980: New Zealand adrift. Wellington, A.H. & A.W. Reed. 442pp.
- Stimac, J.L., Leong, K.L.H., 1977: Factors affecting chironomid larval abundances in three vertical aquatic weed habitats. *Environ. Ent.* 6: 595-600.

- Stubbs, M. 1980: Another look at prey detection by coccinelids. *Ecol. Ent.* 5: 179-182.
- Swammerdam, J., 1675: *Bybel der Natuure*. Leiden. (cited in Corbet 1962).
- Tanaka, Y., Hisada, M., 1980: The hydraulic mechanism of the predatory strike in dragonfly larvae. *Journal of Experimental Biology* 88: 1-19.
- Teramoto, E., 1982: A mathematical model of density dependent dispersive motions. Ch 18 [in] *Biomathematics in 1980*. North Holland.
- Thompson, D.J., 1978a: Towards a realistic predator-prey model: the effect of temperature on the functional response and life history of larvae of the damselfly Ischnura elegans. *Journal of Animal Ecology* 47: 757-767.
- Thompson, D.J., 1978b: Prey size selection by larvae of the damselfly, Ischnura elegans (Odonata: Zygoptera). *Journal of Animal Ecology* 47: 769-785.
- Thompson, D.J., 1978c: The natural prey of larvae of the damselfly, Ischnura elegans (Odonata: Zygoptera). *Freshwater Biology* 8: 377-384.
- Thompson, D.J., 1982: Prey density and survival in damselfly larvae: field and laboratory studies. *Adv. Odonatol.* 1: 267-280.
- Tillyard, R.J., 1913a: On some new and rare Australian Agrionidae (Odonata). *Proceedings of the Linnean Society of New South Wales* 37: 404-479+plates.
- Tillyard, R.J., 1913b: Study of the Odonata of Tasmania. *Proceedings of the Linnean Society of New South Wales* 38(4): 765-778.
- Tillyard, R.J., 1916: The life-histories and descriptions of Australian Aeschnidae. *Journal of the Linnean Society (London) (Zoology)* 33: 1-87.
- Tillyard, R.J., 1917: The biology of dragonflies (Odonata of Paraneuroptera). London, Cambridge University Press. 396pp.

- Tillyard, R.J., 1926: The insects of Australia and New Zealand. Sydney, Angus & Robertson 560 pp.
- Tinbergen, N., 1951: The study of instinct. London, Oxford University Press 228pp.
- Uttley, M.G., 1980: A laboratory study of mutual interference between freshwater invertebrate predators. Unpubl. PhD. thesis Univ. of York
- van Rhijn, J.G., 1980: Communication by agonistic displays. Behaviour 74: 284-293.
- Watson, J.A.L., 1974: The distributions of the Australian dragonflies (Odonata). Journal of the Australian Entomological Society 13: 137-149.
- Watson, J.A.L., 1981: Odonata (dragonflies and damselflies). in A. Keast [ed] Ecological biogeography of Australia. The Hague, W. Junk. pp1141-1167.
- Werner, E.E., Gilliam, J.F., 1984: The ontogenetic niche and species interactions in size-structured populations. Ann. Rev. Ecol. Syst. 15: 393-425.
- White, A., 1843: List of the annulose animals hitherto recorded as found in New Zealand with descriptions of some new species. in Dieffenbach, E., Travels in New Zealand, Vol. 2 pp 265-291. London, Murray.
- Wilson, D.S. 1974: Prey capture and competition in the antlion. Biotropica (6)3: 187-193.
- Wilson, E.O., 1975: Sociobiology. Havard, The Belknap Press
- Wise, K.A.J., 1965: An annotated list of the aquatic and semi-aquatic insects of New Zealand. Pacific insects 7: 191-216.
- Wise, K.A.J., 1977: A synonymic checklist of the hexapoda of New Zealand sub-region the smaller orders. Bulletin of the Auckland Institute and Museum 11, 176pp.

- Wootton, R.J., 1981: Palaeozoic insects. Annual Review of Entomology 26: 319-344.
- Zahner, R., 1959: Über die Bindung der mitteleuropäischen Calopteryx-Arten (Odonata, Zygoptera) an den Lebensraum des stromenden Wassers. I. Der Anteil der Larven an der Biotopbindung. Int. Rev. Hydrobiol. 44: 51-130.
- Zeeman, E.C., 1976: Catastrophe theory. Sci. Am. 234(4): 65-83.

APPENDIX 1

Some data processing techniques

Smoothing

When an inherently continuous variable is made arbitrarily discrete e.g. by the use of a finite decimal representation (as occurs when using any real measuring instrument) a spurious fine structure is generated by the digitising process. Such extraneous, misleading fine structure is commonly removed by 'smoothing' the measured data. Biologists are generally familiar with the 'moving point average' viz

$$x_i^1 = (x_{i-1} + x_i + x_{i+1})/3$$

where each value is replaced by the mean of its own value and the one on either side. When a sampling scheme is regular (divisions equispaced) then it can be shown that the weighted moving average

$$x_i^1 = (x_{i-1} + 3 \cdot x_i + x_{i+1})/5$$

(so called 1:3:1 smoothing) is a close approximation to the best smoothing function. This smoothing removes the contributions of spectral frequencies above the resolving power of the measuring system.

Proof: Consider the conjugate (frequency) domain. The Nyquist sampling theorem holds that under regular sampling all harmonics up to half the sampling frequency are determined. Calculated amplitudes of frequencies above half the sampling frequency are spurious. Removal of these contributions through the application of a sharp cut-off (rectangular) filter with width equal to half the sampling frequency is equivalent in the conjugate (spatial) domain to convolution with a sinc function. Numerical values for the convolving function are close to the 1:3:1 ratio given above. Details of the proof are available in standard texts on digital filtering or fourier optics.

Use of cumulative distributions

When any inherently continuous function is made arbitrarily discrete the possibility of digitising error and censoring arises. If a

function of continuous time is sampled at regular intervals it is impossible to measure lifetimes of events with any greater precision than the sampling interval (i.e. $t_i < \text{lifetime} < t_{i+1}$).

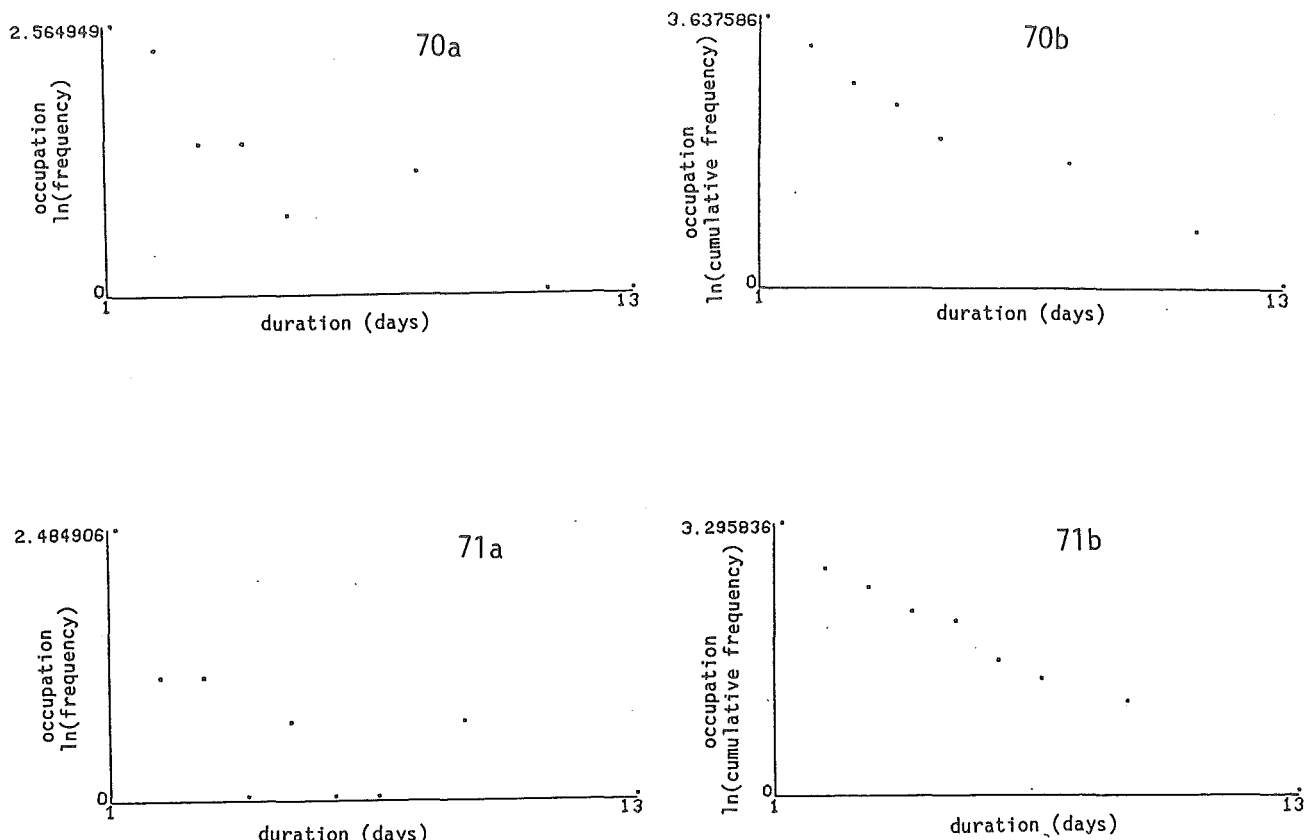
The effects of censoring, of digitising error and of stochastic variations ('noise') in the data can be ameliorated through the use of cumulative functions. Consider $\int (f(t) + g(t))dt = F(t) + G(t)$ where $f(t)$ is the underlying distribution and $g(t)$ represents 'random fluctuations' or 'noise'. Then $E(G(t)) \rightarrow 0$ (approx) and the variance of $G(t) \rightarrow \text{var}(g(t))/N$ where N is the number of contributing samples. By using the cumulative representation a marked improvement in the 'signal' to 'noise' ratio can be effected. The effects of the 'high frequency' components associated with digitising error (above - smoothing) are reduced through the properties of integration in the conjugate domain and censoring ceases to be a problem as the cumulative function is fitted through observed points (and we know that the object existed at time t_i).

Rigorously $g(t)$ (and therefore $G(t)$) is not a Gaussian distributed random variable (because frequency values less than 0 do not occur) therefore $E(g(t))$ and $E(G(t))$ are not 0 and $\text{var}(G(t))$ is not equal to $\text{var}(g(t))/N$. While a detailed proof is beyond me the experimental evidence indicates that the 'approximation' is adequate. The information content is increased through the incorporation of information on order.

Application. Instead of examining the number of occupations which ceased on day T consider the number which survive at least T days. If the population has an underlying negative exponential distribution (Ae^{-kt}) then the interpolating function will be

$$\int_T^{\infty} Ae^{-kt} dt = (A/k)e^{-kT}$$

a negative exponential with the same exponential coefficient (the invariance of functional form under integration is a property unique to exponential functions). Figs 70, 71 demonstrate the effect of using the cumulative distribution on duration of site occupation data.



Figs 70, 71. Comparison of raw frequency and cumulative frequency presentation of data.

Fig 70a. Raw data from occupation of 4.5-mm diameter stems with *Simocephalus* as prey.

$$\ln(\text{frequency}) = 2.34 - 0.197 \times \text{duration}; r = -0.91$$

Fig 70b. Cumulative data from occupation of 4.5-mm diameter stems with *Simocephalus* as prey.

$$\ln(\text{cumulative frequency}) = 3.67 - 0.280 \times \text{duration}; r = -0.99$$

Fig 71a. Raw data from occupation of 4.5-mm diameter stems without prey.

$$\ln(\text{frequency}) = 1.47 - 0.143 \times \text{duration}; r = -0.65$$

Fig 71b. Cumulative data from occupation of 4.5-mm diameter stems without prey.

$$\ln(\text{cumulative frequency}) = 3.31 - 0.259 \times \text{duration}; r = -0.99$$

log transform

Negative exponential distributions are conventionally examined by conducting a linear regression analysis on the log transformed frequency data. Such a regression usually produces an 'adequate' fit to the exponential coefficient but there are problems. The regression on the log transformed data weights data equally whereas the variance of each point estimate is N (the frequency of the observation) (assuming Poisson statistics). Thus large values (those near the 'y' axis) are seriously underweighted and this can have a marked effect on the predicted intercept (and estimate of the original population size). Because of the non linear metric the simple least squares procedure is inappropriate, but this effect will not be significant if departures from fit are small (i.e. when correlation coefficients are large). If the underlying distribution is not a simple exponential then the log transform 'breaks down' e.g.

$$\log(Ae^{-kt}) = \log A + -kt$$

$$\text{but } \log(Ae^{-kt} + b) \rightarrow ?$$

$$\text{or } \log(Ae^{-kt} + Be^{-mt}) \rightarrow ?$$

If one of the factors in the bracket is dominant in some domain then the transformation can be applied in an 'engineering' fashion i.e. the fit will be 'adequate' or asymptotically correct. Interpretation of the transformed data in domains where the factors have comparable effect is problematical.

In the problem being tackled here the 'samples' are 'counts' and are expected to have a Poisson distribution. The standard deviation is thus $N^{\frac{1}{2}}$, and as N increases the distribution approaches a Gaussian distribution. In fitting the log-linear curve, when N becomes 'large' $\log(N \pm N^{\frac{1}{2}})$ is approximately $\log(N)$.

APPENDIX 2

This appendix contains an account of the predatory versatility found in larval Hemianax papuensis. The existence of predatory versatility in Odonata larvae had been indicated by the occurrence of prey-specific behaviours in second instar X. zealandica. The work on H. papuensis confirmed the presence of predatory versatility in Odonata larvae. The appendix is presented in the form accepted by J. Zool. Lond. and follows the conventions of that journal.

Predatory versatility in a larval dragonfly, Hemianax papuensis
(Odonata: Aeshnidae)

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Larvae of the large dragonfly Hemianax papuensis used four disparate, prey-specific predatory behaviours. Arthropod prey moving on a substratum were stalked and then attacked from a distance. Arthropod prey moving in the water column or at the water surface were approached using 'jet' propulsion and then attacked from a distance. Snails, an unusual prey for an arthropod, were stalked; then the larva manoeuvred about them until a specific orientation was achieved before an attack was made from close range. Dead snails were scavenged, using tactics very similar to those used with live snails, but non-snail carrion was rarely taken. There was no evidence that the possession, by H. papuensis, of specialized behaviours for an atypical prey - snails - lowered its success when attacking other types of ('typical') prey.

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Acknowledgments

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Introduction

Although predatory versatility, the use of disparate prey-specific predatory behaviours by euryphagous predators, is documented in several vertebrates, prey-specific behaviours have rarely been recorded in invertebrates (Curio, 1976). Predatory versatility occurs in some orbweb and jumping spiders (Robinson & Olazarri, 1971; Robinson & Robinson, 1976; Suter, 1978; Hill, 1979; Jackson & Blest, 1982; Freed, 1984); but records of insects using prey-specific predatory behaviours are notably scarce (Lawton, 1970; Bay, 1974; Thornhill, 1975). The aims of this study were to examine the predatory behaviours of a larval dragonfly, Hemianax papuensis (Burmeister) (Anisoptera: Aeshnidae: Anactini), and to document evidence of predatory versatility.

There have been several studies of predatory behaviour and the sensory systems used in prey detection by larvae of aeshnid dragonflies (Baldus, 1924; Abbott, 1925; Richard, 1960; 1962; Hoppenheit, 1964; Pritchard, 1964; 1965; Etienne, 1968; 1972; Heymer, 1970; Kime, 1974 and Blois & Cloarec, 1985). From these studies, it is known that vision is primary in prey detection, and predatory behaviour has been envisaged as a reflex response to simple stimuli (e.g. flickering spots of light (Etienne, 1968)).

Larval Odonata usually catch prey by a rapid, hydraulic, extension of the elbowed labium (Corbet, 1962; Tanaka & Hisada, 1980). While in many Odonata larvae the labium and labial palps are modified and apparently adapted to capture particular types of prey, larval Aeshnidae have a simple labium – the prementum is almost planar and the relatively simple labial palps are hinged to move in the plane of the prementum (Fig 1). Aeshnid larvae are commonly regarded as particularly voracious and effective predators.

In Anisoptera (including Aeshnidae) the hydraulic pulse which extends the labium is provided by a muscular diaphragm in the abdomen.

This diaphragm is also used to eject water from the rectum to 'jet' the larva forward. In Aeshnidae this rectal propulsion is powerful (Mill & Pickard, 1975) and is used in rapid escape.

Methods

Final instar larvae of H. papuensis were collected from beds of Elodea canadensis Michx. in a pond at Taupo, North Island, New Zealand (38°42' S 176°06' E). An ovipositing female was obtained at the same site.

Predatory behaviours were observed in large (45 x 30 x 15 cm) and small (15 x 4 x 15 cm) aquaria containing short lengths of plastic, simulated water plants. Prey were introduced to the aquaria at a point as far as practicable from the resident larva. Prey species used in the laboratory were similar to those found in faecal pellets from the field. Some behaviours were analysed from videotapes.

The responses of H. papuensis larvae to different types of prey were tested. Prey moving on a substratum were represented by damselflies (Austrolestes colenisonis (White) (Zygoptera: Lestidae) and Xanthocnemis zealandica (McLachlan) (Zygoptera: Coenagrionidae)), caseless caddis (Trichoptera: Hydrobiosidae, Leptoceridae (with cases removed)) and feeding mosquito larvae Opifex fuscus (Hutton) (Culicid :). Prey found in the water column were represented by actively swimming O. fuscus. Larval Periplaneta americana (L.) (Blattodea: Blattidae), O. fuscus larvae respiring through their anal syphons, larval Stratiomyidae, and blowflies (Calliphora sp.) (Diptera: Calliphoridae), represented prey suspended from or trapped at the water surface. Physa acuta Draparnaud (Gastropoda: Pulmonata), an introduced snail common in the larval habitat of H. papuensis, was used as snail prey.

To test if the specialized behaviours used on snails were learned, a deprivation experiment was performed. H. papuensis larvae were raised from the egg on larval Diptera (Chironomus zealandicus Hudson (Chironomidae) and Opifex fuscus) until the final instar. At no time did they have contact with snails. Availability of these naive larvae

made possible the observation of predation on snails under controlled conditions.

Scavenging was examined using freshly heat-killed A. colenisonis, X. zealandica and P. acuta; unconsumed carcasses were removed after 24 h. Incidental observations were made with decaying O. fuscus.

Dead P. acuta, sealed in 25 x 75 mm vials were used to examine the influence of shape discrimination in inducing snail-specific predatory behaviours and scavenging on snails.

Results

Predatory sequences observed

Typical predatory sequences progressed through distinct phases. The larva detected the prospective prey and ceased other activities (e.g. walking or grooming) then, with a quick movement, it turned its head to face the target. The larva then turned its body towards the prey and moved closer, either walking rapidly towards it, or stalking (with its body lowered against the substratum and pausing, in a low crouch for several seconds at a time during the approach). When it was within striking range of the prey the larva adjusted its position relative to the prey and then attacked. Feeding followed.

Sequences varied somewhat depending on details of the encounter. All larvae examined used all the responses appropriate to the prey types they were exposed to, but some appeared to be more 'adept' than others with different kinds of prey. When stalking prey, H. papuensis larvae ignored distractions, including other potential prey items passing close by. Even escape responses to interference by the experimenter appeared to have a much higher threshold while larvae were stalking prey.

Predation on mobile arthropods moving on a substratum (Fig. 2)

Larvae typically responded to prey 50–100 mm away. Prey were stalked with the larva alternately moving in short rushes and crouching close to the substratum for a few seconds. The larva continued stalking stationary prey, but the approach was slower than when the prey was moving.

When a larva was close enough to make a labial strike, it usually slowed for a few seconds and briefly adjusted its position. Immediately (0.04–0.08 s) before the labial strike the larva rocked its body forwards toward the prey. Labial strikes usually occurred near the maximum range of the labium, were fast (about 0.02 s), and appropriately ranged. In a few strikes, the labium was only partially extended, and these too were

ranged to strike the prey and not to overshoot it.

This sequence of behaviours was used against damselfly larvae and caddis larvae and when attacking mosquito larvae which were either swimming slowly over the substratum or were stationary while feeding at the substratum. H. papuensis larvae unable to reach prey because of a break in the vegetation did not swim across the gap but instead detoured and used an indirect route. Mosquito larvae which swam actively past the larva were captured after an unconcealed rush across the intervening vegetation and without any apparent pause to orientate at the end of the movement.

Predation on arthropods swimming in the water column or suspended from the surface (Fig. 3)

H. papuensis larvae responded rapidly to mosquito larvae hanging from their anal siphons at the surface. The dragonfly larva made a quick, vertical movement of the head to face the prey and then attempted to stalk or rush the prey by moving across vegetation. If it was unable to get within range for a labial strike while retaining contact with the substratum (even if only with the hind legs), the larva drew back for a few seconds to hold the substratum with all 6 legs. It then 'rushed' the prey. As soon as it lost contact with the substratum the larva swam, using controlled rectal 'puffs' to drive itself at the prey. When it was within labial-strike range of the mosquito, it attacked. If the attack was unsuccessful the larva sank slowly for a few seconds while swimming with its legs and reorientated before again using rectal propulsion to close on the prey.

When mosquitoes swimming in open water approached a perched larva at the same level, the larva launched itself with a single, powerful 'puff' and then coasted ballistically to the prey. Immediately after striking and capturing the prey, the larva turned by swimming (using its legs) and then used rectal propulsion to return to its perch.

Larval Stratiomyidae or terrestrial arthropods trapped on the surface were attacked without the preliminary attempts to stalk or rush seen with mosquitoes. As the prey drifted slowly across the surface the predator turned its head rapidly toward it and then launched itself into the water column. Terrestrial arthropods trapped at the water surface seemed to attract the dragonfly's attention by the vibrations produced as they struggled. H. papuensis larvae reacted and moved towards the source of the vibrations before they could have seen the prey.

Predation on live snails (Figs 4, 5)

When a snail moved into view, the larva turned rapidly toward it and then began to stalk. On coming into range for a strike, the larva stopped advancing and began to manoeuvre first its head and then its body, adjusting its own orientation relative to that of the moving snail. The larva moved slowly closer as it manoeuvred until the snail was less than half the length of the labium away. When the snail was broadside on to the larva and the larval labium was in the same plane as the foot of the snail, H. papuensis paused for a few seconds and then attacked. Attacks on medium to large snails (shell length > 5 mm) differed from those seen with other prey: the larva rocked its body slightly forward without moving its feet, opened its labial palps, and then struck and grasped the snail about the 'neck' between the muscular foot and the shell. This labial strike was slower than that used against other types of prey and the larva's body lunged forward so that the mouthparts came into contact with the snail within 0.04–0.1 s of the strike. Snail killing may have involved further specialized behaviours because snail bodies went limp within a few tenths of a second of capture; in contrast, snails grasped in forceps struggled for several seconds. The snail was then held against the mouthparts and consumed.

Snail prey were secured by one labial palp which held the outside

of the shell, and were then removed from the shell by scraping movements of the maxillae. First, the body was eaten out of the shell and then the foot was consumed, after which the empty shell fell away. On occasions the mandibles and the free labial palp were used to remove the flesh.

H. papuensis larvae had an alternative tactic for extracting snails from their shells, but during this study this was used only on large, empty shells. The labium grasped the shell and manoeuvred it against the mandibles as chunks were 'nibbled' from a localized area on the edge of the shell (Fig. 6). This method of extraction seemed to be very time-consuming. As it was never observed being used on live or dead snails and is seldom needed with snails like P. acuta.

The complex manoeuvres observed as larvae sought the appropriate attack position for snails were distinctly unlike those seen with other prey. Larvae twisted and turned their bodies, sometimes for minutes at a time, and scrabbled with their legs while they attempted to adjust their position at the side of the snail. As well as orientating themselves toward the snail, larvae lowered the fore part of their bodies, which improved the line of attack on the 'neck' of the snail. Successful attacks were made from either side of the asymmetrical opening of the snail shell.

Larvae unable to position themselves correctly relative to the snail after several minutes of futile manoeuvring, sometimes attacked anyway. Such attacks were almost always unsuccessful. Snails attacked on the front or rear of the foot were able to withdraw into the shell and the larva retained and consumed only a small piece of tissue torn off by the labial palps. Strikes which hit part of the shell usually failed because the snail almost invariably slipped out of the larva's grasp and then sank to the bottom.

Snails and empty snailshells falling through the water column were pursued rapidly whereas small stones were not. As soon as the snail hit

the floor of the aquarium the larva paused and then began to stalk, even before the snail had begun to emerge from its shell.

Small (<3 mm shell length) snails were attacked after a sequence of behaviours similar to those used when attacking arthropods; however the labial 'strike' was, again, from closer range and slower than that observed with other prey. If a snail was caught by the foot the body was eaten out while the labium and labial palps manipulated the shell, rather like someone eating an icecream cone. If a small snail was caught by the shell it was lifted to the mouthparts and attacked by mandibles and maxillae while the labium pressed the snail towards the mouth. The shell was broken within seconds and the flesh inside was then consumed.

Snails were attacked from a significantly shorter range than were other prey (Mann-Whitney U-test; $P < 0.001$) (Fig. 7).

Naive larva feeding on live snails

Some days after moulting to the final instar, a naive larva was offered a medium-sized snail, (*P. acuta*, shell length about 7 mm), as prey for the first time. The larva immediately performed the complete pattern as described above. The larva stalked the snail, manoeuvred about the prey, then moved its labium to grasp at the 'neck'. After catching the snail, the larva 'peeled' the body out of the shell.

Scavenging on dead snails

On two successive days five heat-killed medium-sized (mean shell length 7.5 ± 0.9 mm SD) snails were placed in an aquarium without attracting the attention of the resident larva. The snail shells were all empty 24 h later. When the aquarium was examined on the second day, the larva was facing the opening of a (now empty) snail shell at a distance of about 10 mm. Two further dead snails were introduced to the aquarium without attracting the larva's attention, and several small (shell length < 2 mm) live snails were added to excite larval movement. When observation resumed 20 min later, one carcass had been eaten and the

larva was facing the full shell. The larva was manoeuvring its body to orientate on the opening of the snail shell, and reaching out and grasping at the opening with its labium and labial palps. This appeared to be a muscular movement rather than the hydraulic mechanism used in a labial strike. The snail body moved along the glass floor of the aquarium as it slid from the grasp of the larva, and the larva followed, reorientated and grasped at it repeatedly.

To find which sensory modality was used by H. papuensis to recognize snails, a dead snail was sealed in a glass vial filled with water and sunk in the aquarium. Within 30 min the larva was alongside the vial and attempting to orient itself so as to make the final approach (which was impossible because of the vial); the larva gave up its attempts after another 30 min. This larva manoeuvred into an attacking position at the vial several times over the next few days, even after the water in the vial had become turbid as the snail decayed.

Scavenging on dead arthropods

Five antepenultimate-instar larvae of A. colenisonis and 1 final instar larva of X. zealandica were killed and placed in a small aquarium with an H. papuensis larva that had scavenged on snails. The carcasses were replaced daily. In 5 days only one A. colenisonis was eaten (the behaviours involved were not observed); the other carcasses had not been touched.

During experiments with mosquito larvae, a few dead, intact bodies, black with putrefaction, were introduced inadvertently to an aquarium. One of these bodies came to rest a few centimetres from an H. papuensis larva and swayed slightly in the water column. After a few seconds the dragonfly approached the carcass and struck with its labium. The carcass was moved to the mandibles and the head and thorax were consumed within seconds. The larva stopped suddenly and remained motionless for about 5 s. It then extended its labium a few millimetres, opened the labial palps

and released the disintegrating abdomen of the carcass. After most of the carrion had been extracted, it began intensive cleaning motions with its labium and maxillary palps, which cleared away the remaining uningested pieces. For several minutes after this intensive cleaning, the larva did not respond to prey but remained in the same place and occasionally cleaned its mouthparts with movements of the labium.

Discussion

H. papuensis larvae occur in the weed zone of ponds and temporary waters throughout the Australian continent (Tillyard, 1916) and locally in Tasmania and New Zealand (Rowe, in press). The larvae are active predators with acute vision and seem to be ecologically similar to the Anax species investigated by Kime (1974) and Johnson & Crowley (1980). With its high growth rate (e.g., from 2.5 mm to 45 mm long in <195 days at 20°C) and high thermal coefficient of growth (Hodgkin & Watson, 1958; Rowe, unpubl. data), the species is well adapted to life in temporary waters.

Animals which depend on ephemeral habitats must be able to complete development within the expected lifetime of the habitat. In such habitats the ability to capture a variety of different prey would probably be highly advantageous. Furthermore, the use of active, cursorial hunting tactics would increase the rate of contact with potential prey and would also be advantageous to an animal developing under a severe time constraint. The difference in hunting tactics between the two tribes of the Aeshninae (Davies, 1981) may be due to the action of such selection pressures. Larval Aeshnini (Aeshna sp.) are cryptic, sit and wait, ambush predator inhabitants of permanent waters which occasionally, when very hungry, stalk prey, or even use rectal propulsion to attack prey in midwater (Richard, 1960; 1962; Pritchard, 1965; Rowe, unpubl. obs.). In contrast larval Anactini (H. papuensis and Anax sp.) are unconcealed, active predators, stalking and pursuing prey even when nearly satiated.

Blois (1985) analysed the predatory behaviour of Anax imperator Leach (Anisoptera: Aeshnidae) larvae feeding on a variety of prey species. Using factorial analysis of correspondence she found prey specific differences in the frequency of occurrence of behaviour sequences.

The behaviour sequences used by H. papuensis were well matched to the prey attacked. Mobile and evasive prey were stalked and then attacked swiftly from near the maximum range of the labium. By striking from a distance the larva gives prey little time to avoid the attack (about 0.02s: Pritchard, 1965; this study). H. papuensis larvae stalking prey, but unable to get close because of a break in the vegetation, did not swim across the gap; instead they moved away until they reached an alternative route and then resumed the stalk. This behaviour presumably reduced the probability of alarming the prey. (Detouring as a predatory tactic is known in some vertebrates (Curio, 1976) and in the Salticidae (Araneae) (Hill, 1979), but this is the first indication I know of in insects.)

Actively swimming prey were approached without caution. The rush used to approach such prey may be concealed by the prey's own chaotic sensory environment. When, however, the same prey were immobile in the water, H. papuensis larvae attempted to stalk them, and only swam if no walking path was available. Attacks on mosquito larvae floating in open water were made from below, where the dragonfly could intercept escape movements. Arthropods trapped by the surface tension could not escape and were approached directly, without any attempt at concealment.

A rapid response to the presence of terrestrial arthropods trapped at the water surface would be highly adaptive because such items are often more or less incapacitated. Access to trapped terrestrial arthropods on the surface is probably restricted to the 'top' predator(s) in any system. An animal which is not immune to attack would itself be at risk to 'top' predators attracted to the struggling prey. In permanent waters, some fish use this food source but predatory fish are usually absent in temporary habitats and larval Anactinae are frequently the 'top' predators. The high susceptibility of larval Anactinae to predation by fish which has been observed (Kime, 1974; Johnson & Crowley, 1980;

Folsom & Collins, 1982; Rowe, in press) may be associated with their conspicuous behaviour.

Records of predation on snails by larval Odonata are fragmentary. Needham & Hart (1901), Williams (1936), Yamaguchi (1963), Pritchard (1964), Pfau (1967), Miyakawa (1969), Sievers & Haman (1973), Folsom & Collins (1982) and Stark (1981) recorded the occurrence of snail remains (eggs, shell fragments or raduli) in gut or faecal pellet contents. There is little information on specialized snail predation tactics in larval Odonata. Sievers & Haman (1973) noted that, in contrast to Williams' (1936) account of Anax strenuus Hagen breaking up snail shells, Anax junius Drury "peeled" the snail from its shell, leaving the shell intact. Blois (1985) found that predation on snails by A. imperator took longer than attacks on other prey types and involved extensive sequences of manoeuvring behaviours. The behaviour of A. imperator described by Blois differs from that of H. papuensis in the labial strike being directed at the anterior of the snail's foot, in the larva eating the snail body in situ from the shell and in the extremely long duration of the prey consumption phase (about 44 min.). Corbet (1962) speculated that species which used vision for prey detection through the day might descend from plants to the benthic sediments and use other receptors for prey detection at night. He felt this could account for the otherwise inexplicable presence of aquatic gastropods in the diet of Anax larvae. Snails are abundant in temporary ponds in northern Australia (Blair & Finlayson, 1981) which probably represent the archetypal H. papuensis habitat and provide a large potential source of prey.

In contrast to the variable behaviours H. papuensis displayed when attacking arthropods, attacks on large snails were stereotyped. Successful attacks were always directed at the 'neck'. In the laboratory, H. papuensis was generally successful when stalking snails. In nature,

because there are more footholds in the weed, H. papuensis larvae might be even more proficient. The size of snails which were successfully stalked and captured, and the large amount of food obtained from each, indicate there would be considerable adaptive value in the evolution of snail-capturing tactics.

Because larvae peel the snail body from the shell, snail consumption is likely to be underestimated in feeding studies where shell fragments only are sought. Snail eating may prove to be more widespread and common among Odonata larvae than has been considered previously.

Blois and Cloarec (1985) tested prey choice in Anax imperator Leach (Anisoptera: Aeshnidae) larvae. Despite their evidence for snails being a common prey in the field they were unable to obtain predation on snails in the laboratory. This failure was probably a consequence of their experimental method. If, like H. papuensis, A. imperator larvae 'lock on' to, and pursue, an individual prey item then active prey species which 'advertise' themselves through incautious movements will suffer disproportionately in choice experiments at high prey densities. The adaptive value of concentrating on a solitary target is obvious. However, the neural processes involved in selection of stimuli and retaining a stable focus of attention may be extremely complex (Andrew, 1983).

Pritchard (1965) proposed that prey must move to elicit predatory behaviour from dragonfly larvae, and this view has been widely accepted (but see Corbet, 1962). My observations demonstrated that H. papuensis larvae recognize shapes and stalk immobile prey: larvae stalked motionless, empty snail shells and dead snails sealed in containers as they would live snails; dead snails were attacked using a muscular movement of the labium similar to that used for live snails, the only observed difference being that attacks were directed at the shell opening and not at the 'neck'. Furthermore, as snails were 'recognized' from many

different perspectives, it appears that the larvae have some general 'template' for what 'constitutes' a snail. Prey recognition by these keen-sighted predators is a complex process.

Given that H. papuensis has proved to be a larval insect with predatory versatility of some complexity, why are there not numerous other examples in the literature? Perhaps because in previous investigations integrated prey-specific behaviours have been either not expected, or of little, or no, interest, and experiments and observations have not been designed in a manner that would reveal these behaviours.

In invertebrates, as in vertebrates, predators are more likely to have behavioural flexibility than are herbivores. Selection pressures on euryphagous predators occupying temporary habitats with variable lifetimes, would be expected to place a premium on rapid development. Under such conditions it would be advantageous for predators to glean all possible food, and I predict that predatory versatility will be widespread among euryphagous insect predators dependent on temporary habitats.

More generally I suspect that the failure to seek examples of predatory versatility may be a consequence of working in an "optimal foraging" framework and being overly mindful of the adage "A Jack of all trades is master of none". The assumption of handicap implicit in the adage is hard to support when, for the most part, predatory versatility involves the use of 'standard' motor patterns either in different combinations or under the control of different releasers or threshold levels. Predatory versatility may be widespread in euryphagous insect predators.

REFERENCES

- Abbott, C.E. (1925). The relative importance of vision and the chemical sense in Anax larvae. Psyche 32: 315-318.
- Andrew, R.J. (1983). Attention and information storage. Abstr. 10th Int. Ethol. Conf.: 10.
- Baldus, K. (1924). Experimentale Untersuchungen über die Entfernungslokalisation der Libellen (Aeschna cyanea). Z. vergl. Physiol. 3: 475-505.
- Bay, E.C. (1974). Predator-prey relationships among aquatic insects. Ann. Rev. Ent. 19: 441-453.
- Blair, D. & Finlayson, C.M. (1981). Observations on the habitat and biology of a lymnaeid snail, Austropeplea vinosa (Gastropoda: Pulmonata), an intermediate host for avian schistosomes in tropical Australia. Australian J. Mar. Freshw. Res. 32: 757-767.
- Blois, C. (1985). Variations of predatory behaviour in Anax imperator larvae in relation to different prey types. Biol. Behav. 10: 183-214.
- Blois, C. & Cloarec, A. (1985). Influence of experience on prey selection by Anax imperator larvae. Z. Tierpsychol. 68: 303-312.
- Corbet, P.S. (1962). A biology of dragonflies. London: Witherby.
- Curio, E. (1976). The ethology of predation. New York: Springer-Verlag.
- Davies, D.A.L. (1981). A synopsis of the extant genera of the Odonata. Utrecht: Societas Internationalis Odonatologica
Rapid Communication 3.
- Etienne, A.S. (1968). Die Beantwortung von flimmerfrequenzen durch die Libellenlarve Aeschna cyanea M. Z. Vergl. Physiol. 61(1) 34-40.
- Etienne, A.S. (1972). The behaviour of the dragonfly larva Aeshna cyanea M. after a short presentation of a prey. Anim. Behav. 20: 724-731.

- Folsom, T.C. & Collins, N.C. (1982). Food availability in nature for the larval dragonfly Anax junius (Odonata: Aeshnidae). Freshwater Invertebrate Biology 1(3): 33-40.
- Freed, A.N. (1984). Foraging behaviour in the jumping spider Phiddipus audax: bases for selectivity. J. Zool., Lond. 203: 49-61.
- Heymer, A. (1970). Die funktion der Kaudalstecheln bei Aeschna-larven beim beutefang und aggressionsverhalten <Odon. Anisoptera>. Ann. Soc. Ent. Fr. (n.s.) 6(3): 637-645.
- Hill, D.E. (1979). Orientation by jumping spiders of the genus Phidippus (Araneae: Salticidae) during the pursuit of prey. Behav. Ecol. Sociobiol. 5: 301-322.
- Hodgkin, E.P. & Watson, J.A.L. (1958). Breeding of dragonflies in temporary waters. Nature 181: 1015-1016.
- Hoppenheit, M. (1964). Beobachtungen zum Beutefangverhalten der Larve von Aeschna cyanea Mull. (Odonata). Zoologischer Anzeiger 172: 216-232.
- Jackson, R.R. & Blest, A.D. (1982). The biology of Portia fimbriata, a web building jumping spider (Araneae, Salticidae) from Queensland: utilization of webs and predatory versatility. J. Zool., Lond. 196: 255-293.
- Johnson, D.M. & Crowley, P.H. (1980). Odonate "hide and seek": Habitat-specific rules? in Kerfoot, W.E. [ed] Evolution and ecology of zooplankton communities. Spec. Symp. Vol. 3, Amer. Soc. Limnol. Oceanogr. Hanover NH: University Press of New England pp 569-579.
- Kime, J. (1974). Ecological relationships among three species of aeshnid dragonfly larvae. unpubl. PhD. thesis University of Washington. 142pp.
- Lawton, J.H. (1970). Feeding and food energy assimilation in larvae of the damselfly Pyrrhosoma nymphula (Sulz.) (Odonata: Zygoptera). J. Anim. Ecol. 39: 669-689.

- Mill, P.J. & Pickard, R.S. (1975). Jet-propulsion in Anisopteran dragonfly larvae. J. comp. Physiol. 97: 329-338.
- Miyakawa, K. (1969). A study of the life-history of Pseudothemis zonata (Burm.) (Odonata, Libellulidae) II. immature stage. Kontyu 37(4): 409-422.
- Needham, J.C. & Hart, C.A. (1901). The dragonflies of (Odonata) of Illinois: Part 1. Petaluridae, Aeshnidae and Gomphidae. Illinois St. Lab. Natur. Hist. 6: 1-95.
- Pfau, H.K. (1967). A larva of Aeschna cyanea eats gastropod eggs. Tombo 10(1-4): 25.
- Pritchard, G. (1964). The prey of dragonfly larvae in ponds in northern Alberta. Can. J. Zool. 42: 785-800.
- Pritchard, G. (1965). Prey capture by dragonfly larvae. Can. J. Zool. 43: 271-289.
- Richard, G. (1960). Les bases sensorielles du comportement de capture des proies par diverses larves d'odonates. J. Psychol. norm. path. 1: 95-107.
- Richard, G. (1962). Contributions a l'etude ethologique des odonates. Proc. XIth Int. Congr. Ent. Vienna 11(1): 604-607.
- Robinson, M.H. & Olazarri, J. (1971). Units of behavior and complex sequences in the predatory behavior of Argiope argentata (Fabr.). Smithson. contrib. Zool. No. 65.
- Robinson, M.H. & Robinson, B.R. 1976. Discrimination between prey types: an innate component of the predatory behaviour of araneid spiders. Z. Tierpsychol. 41: 266-276.
- Rowe, R.J. (in press). The dragonflies of New Zealand. Auckland: Auckland University Press - Oxford University Press.
- Sievers, D.W. & Haman, A.C. (1973). Notes on snail feeding behavior of Anax junius (Drury): (Odonata). Proc. Iowa Acad. Sci. 79: 105-106.

- Stark, J.D. (1981). Trophic relationships, life-histories and taxonomy of some invertebrates associated with aquatic macrophytes in Lake Grasmere. unpubl. PhD. thesis University of Canterbury, Christchurch. 256pp.
- Suter, R.B. (1978). Cyclosa turbinata (Araneae, Araneidae): prey discrimination via web-borne vibrations. Behav. Ecol. Sociobiol. 3: 283-296.
- Tanaka, Y. & Hisada, M. (1980). The hydraulic mechanism of the predatory strike in dragonfly larvae. J. exp. Biol. 88: 1-19.
- Thornhill, R. (1975). Scorpionflies as kleptoparasites of web-building spiders. Nature 258: 709-710.
- Tillyard, R.J. (1916). The life-histories and descriptions of Australian Aeschnidae. J. Linn. Soc. (London) (Zoology) 33: 1-87.
- Williams, F.X. (1936). Biological studies on Hawaiian water-loving insects: Part II. Odonata or dragonflies. Hawaiian ent. Soc. Proc. 9: 273-349.
- Yamaguchi, M. (1963). Observations on the emergence and adult behaviour of Orthetrum triangulare melania Selys. Tombo 6(1-2): 13-15.

Captions.... Rowe.... Hemianax papuensis

Fig. 1. Dorsal view of the prementum and labial palps of a final-instar H. papuensis larva. The arc of palp opening/closing and the gape are indicated with dashed lines. Scale bar = 5 mm.

Fig. 2. Sequence of predatory attack on an A. colenisonis larva walking across a substratum. Frame numbers indicated (25 frames s^{-1}). (a) H. papuensis larva faces prey (and 'locks on'). (b), (c) minor postural adjustments occur as the (keen sighted) prey slowly advances. Once the prey is appropriately positioned the H. papuensis larva 'rocks forward' (d) and (e) opens its labial palps before striking (f), drawing the prey back to its mouthparts (g), (h) and feeding (i).

Dashed lines indicate movements which occurred between the two interlaced scans comprising a frame (time resolution 0.02 s). (Tracings from video frames.)

Fig. 3. Sequence of predatory attack on an O. fuscus larva swimming through midwater. Frame numbers indicated (25 frames s^{-1}). (a) H. papuensis larva faces prey (and 'locks on'). (b), (c) H. papuensis 'tracks' prey before advancing (d), positioning itself (e) then lunging and striking at the prey (f). (Tracings from video frames.)

Fig. 4. Sequence of predatory attack on a P. acuta moving over a substratum. Frame numbers indicated (25 frames s^{-1}). (a) H. papuensis larva faces prey (and 'locks on'). (b), (c), (d), (e) H. papuensis manoeuvres to, and around, snail. The larva opens its labial palps (f) and 'rocks forward' (g) before grasping the snail (h) and eating (i) into the body (Tracings from video frames; foot of snail stippled.)

Fig. 5. Lateral view of final stages of a predatory attack on a P. acuta the larva is positioned with its labium in the same plane as the foot of the snail. Frame numbers indicated (25 frames s^{-1}).

(a) labial strike at prey. The prey was grasped (b) and the dragonfly larva plunged its head into the shell (c). In (d) (0.28 s after the strike) the limp foot of the snail hangs below the dragonfly's labial palps. (Tracings from video frames; foot of snail stippled.)

Fig. 6. Snail shell (length 1 cm) after being 'nibbled' open by an H. papuensis larva. In this study, as discussed in the text, H. papuensis larvae removed P. acuta bodies directly from their shells and the slower shell nibbling behaviour was used only on empty shells.

Fig. 7. Range to prey at the launching of the labial strike (by one larva). Mosquito prey upper, snails lower. The range (= labial extension required) was measured in terms of larval head lengths to compensate for scale and perspective changes. Only attacks near plan or lateral view were measured. (From video frames.)
Mann-Whitney $U = 136$, $n_1 = 17$, $n_2 = 8$, $p < .001$.

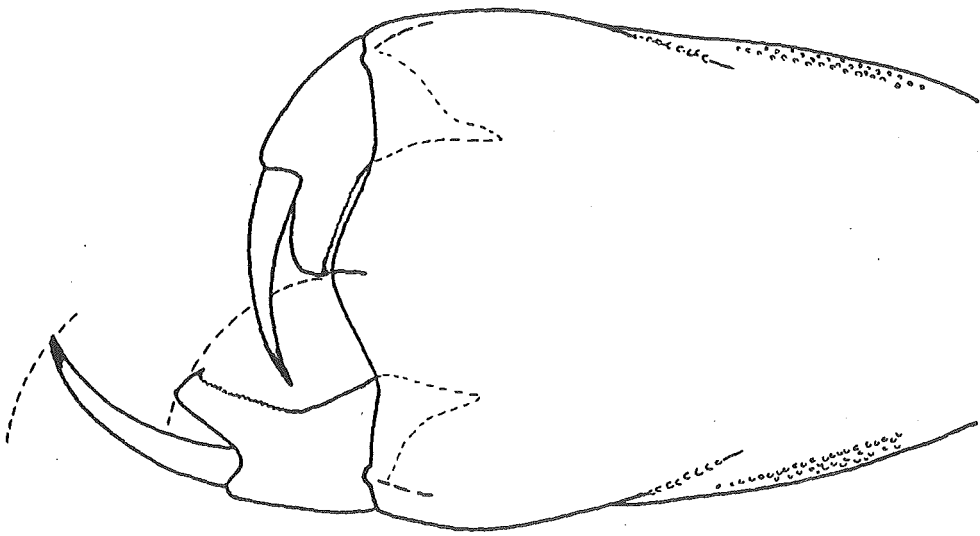


Fig. 1.



Fig. 2.

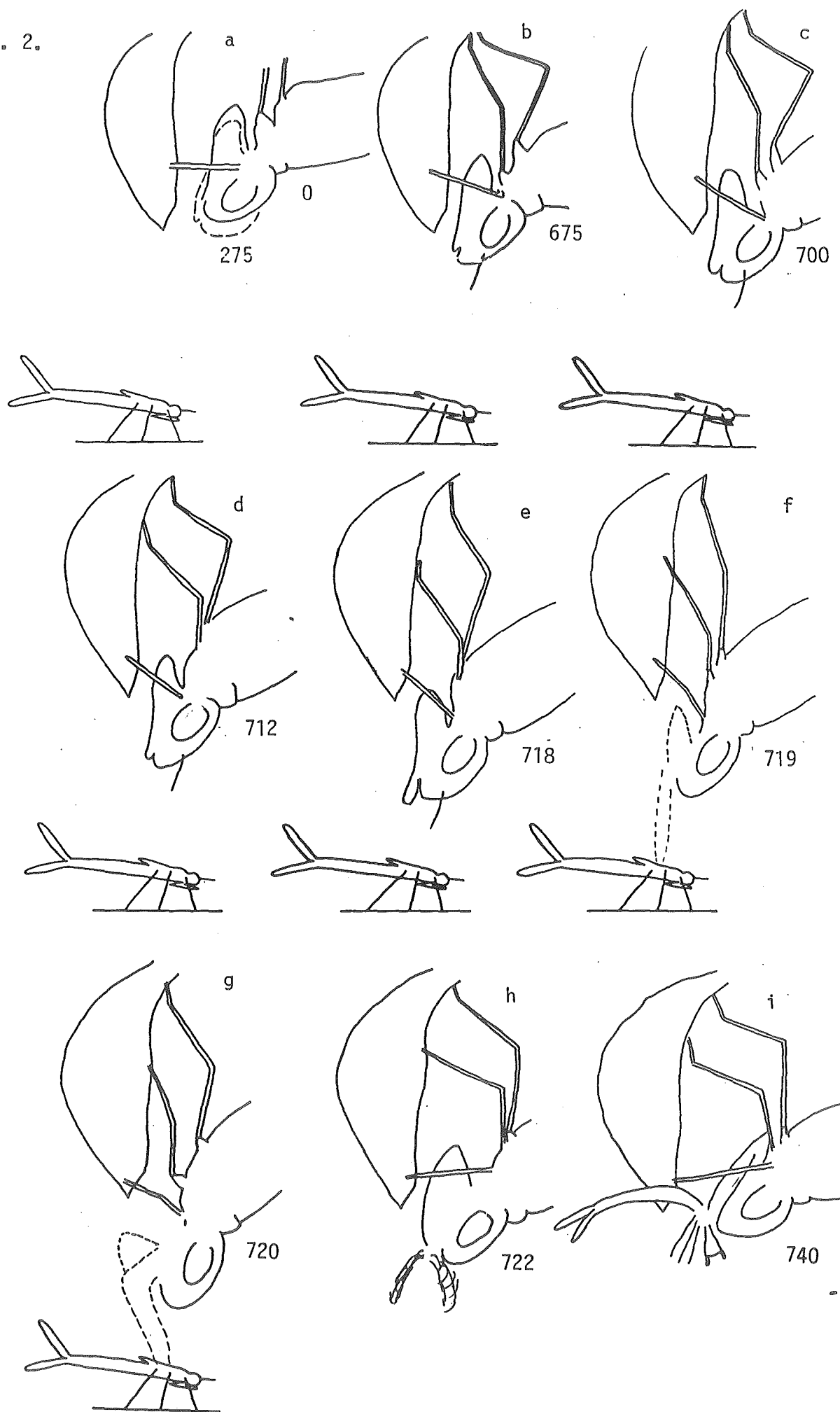


Fig. 3.

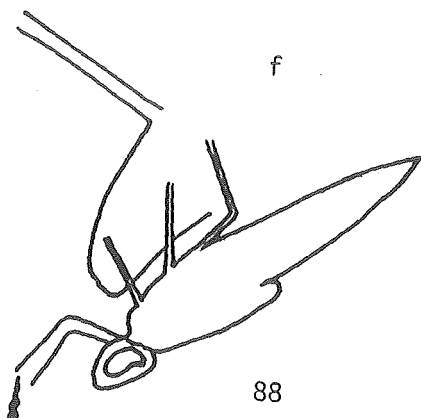
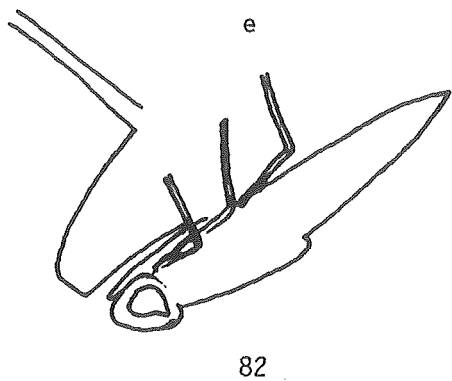
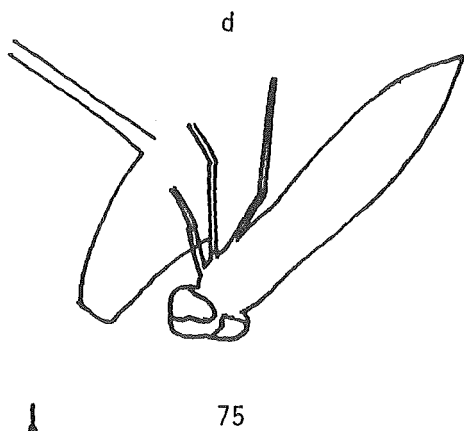
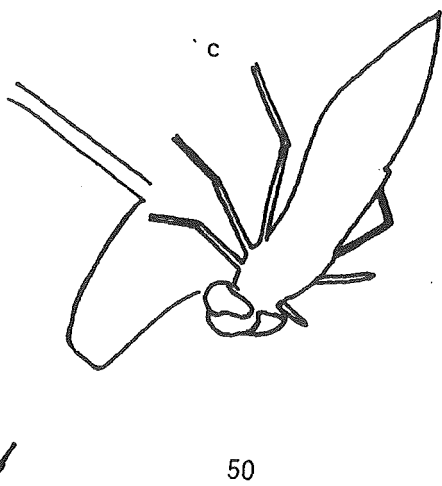
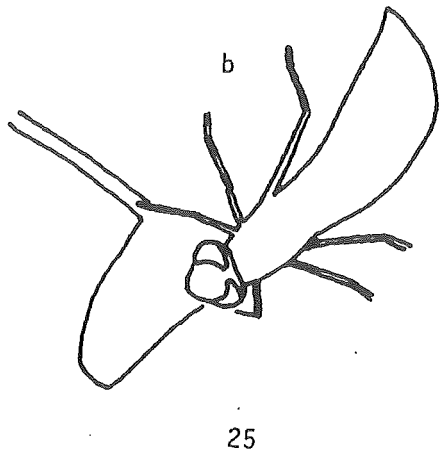
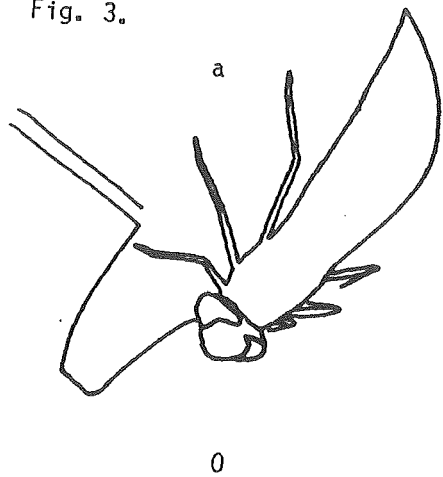


Fig. 4.

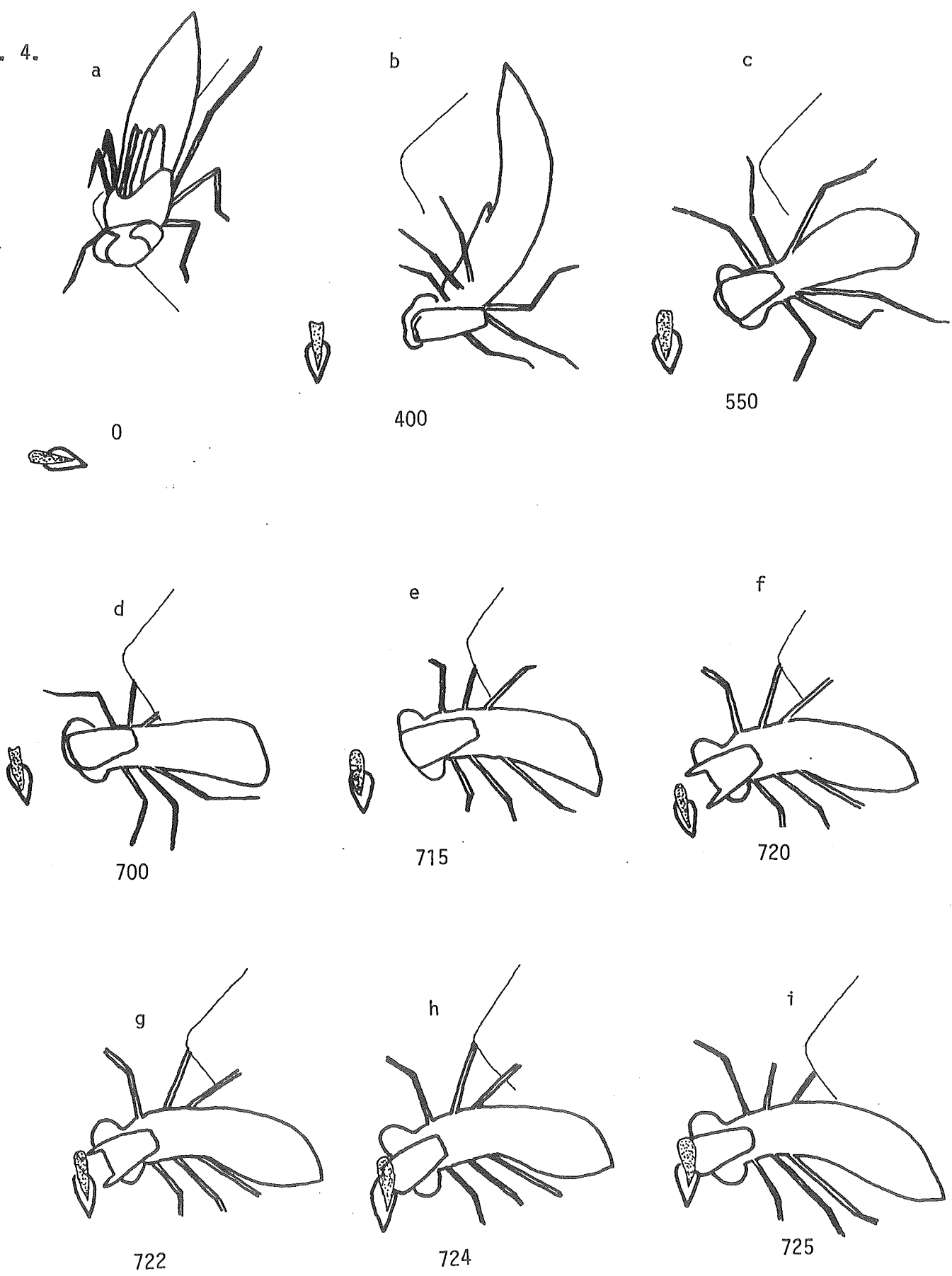
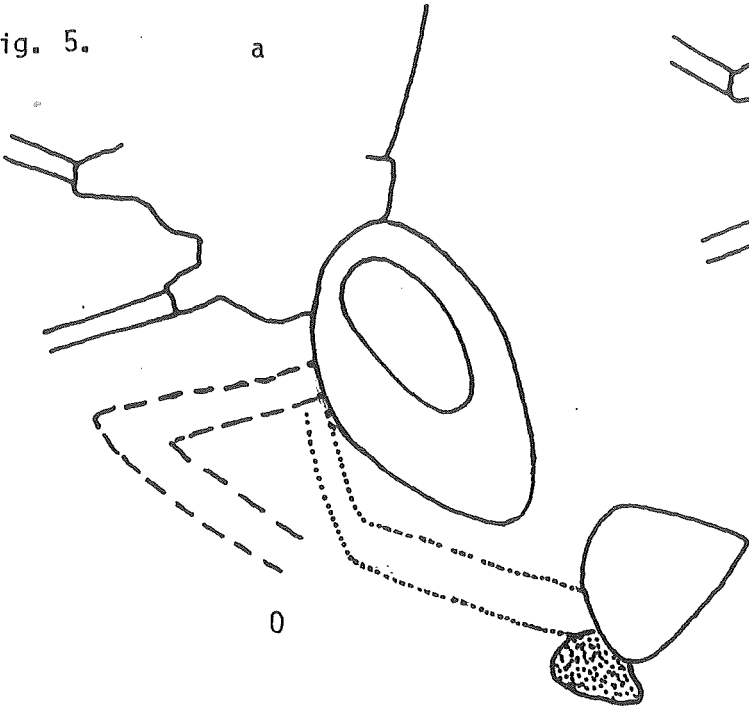
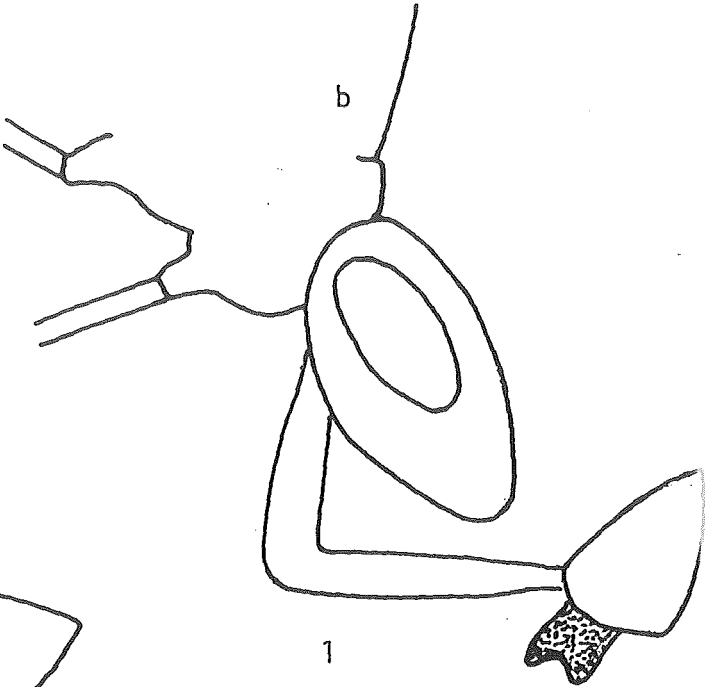


Fig. 5.

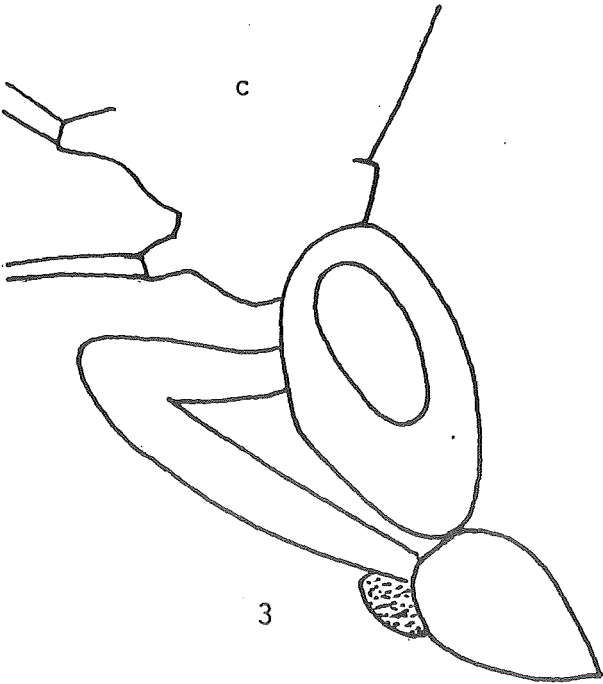
a



b



c



d

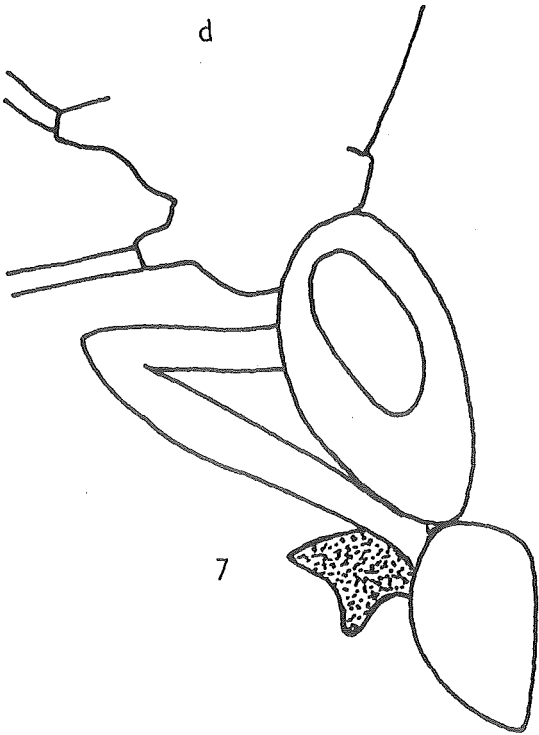


Fig. 6.

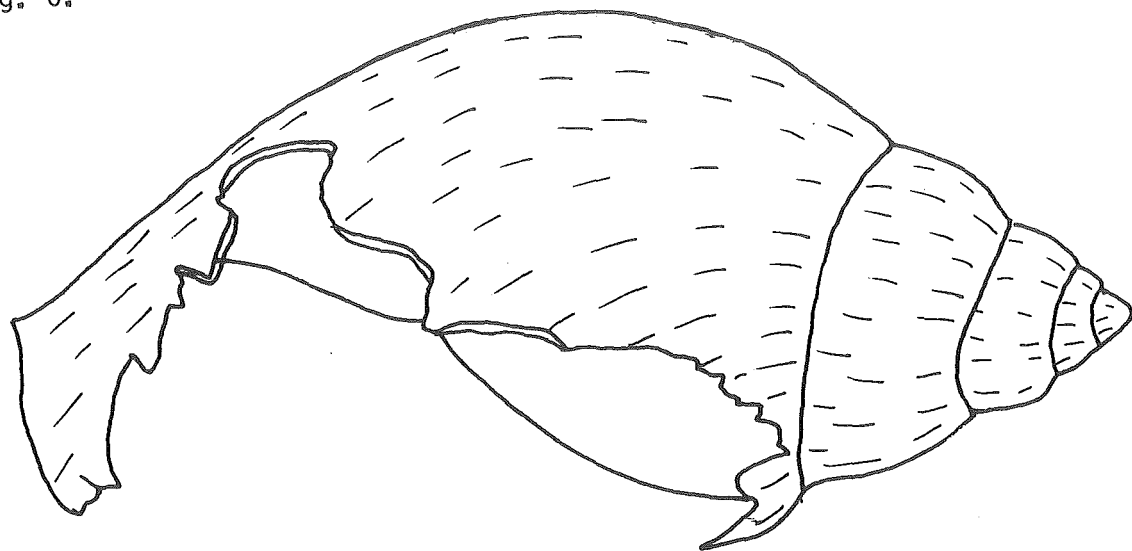
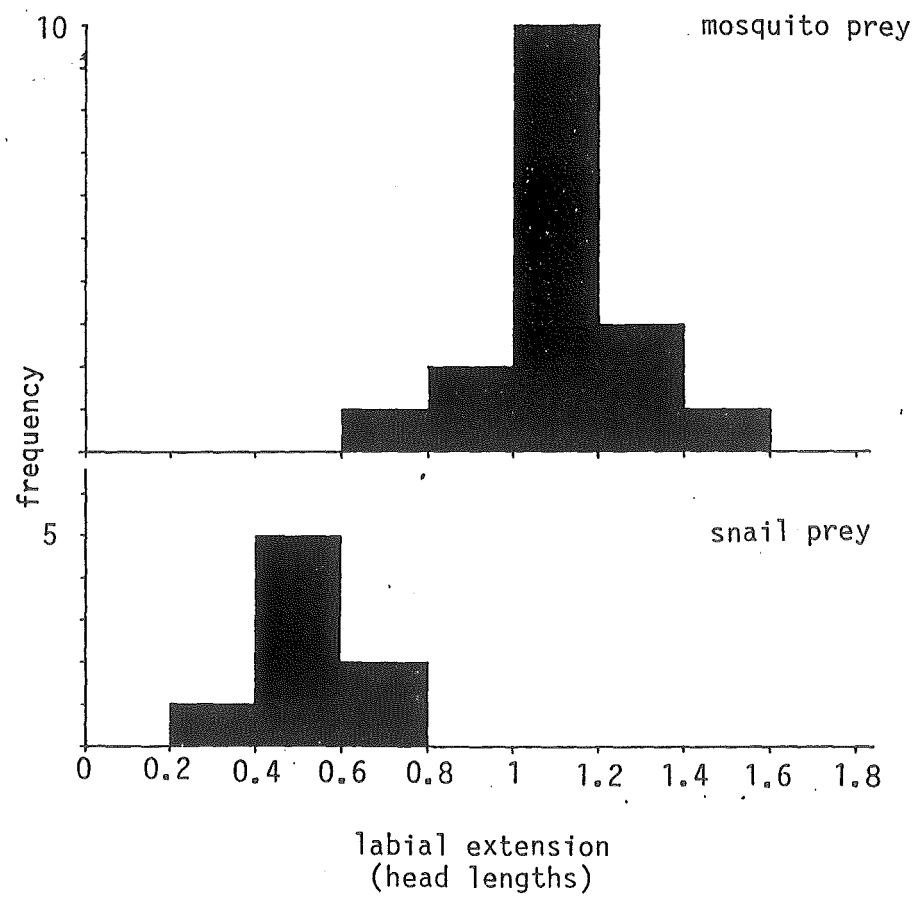


Fig. 7.



APPENDIX 3

This appendix comprises a brief, mathematical treatment of the effect changing diameter has on the usefulness of a stem as a predatory site and as a predator avoidance refuge. Because of the X. zealandica larva's habit of sitting at the base of stems facing downwards it is possible to regard their perches as cylinders with the diameter the only parameter of interest. Predatory activity can be regarded as restricted to a sector of an annulus coaxial with the stem.

Geometry

For a sector of an annulus, major radius $R+r$, minor radius r , subtending an angle θ :

$$\text{Area} = (\theta)/2 \times ((R+r)^2 - r^2)$$

$$(\text{exterior}) \text{ curve length} = \theta \times (R + r) + 2R$$

Stem diameter and predatory activity

Consider the case of a larva on a perch radius r ; able to move a lateral step distance ' s ' and reach radially a distance ' R ' then the subtended angle $\theta = s/r$. If prey is taken from an area then the prey capture area is the sector of an annulus.

$$\text{Area} = s/(2r) \times (R^2 + 2rR) \dots \dots \dots 2$$

The prey capture area is then

$$\min((\pi/2 \times (R^2 + 2rR)), (s/2r \times (R^2 + 2rR)))$$

(The minimum is required because overlapping access does not increase area available.)

For maximum prey capture area:

$$\pi/2 \times (R^2 + 2rR) = s/2r \times (R^2 + 2rR)$$

whence $r' = s/\pi$ (or alternatively s (step) = circumference/2)

If prey is taken as it crosses the exterior boundary of the capture area then prey capture depends on the length of (convex) boundary.

$$= s/r \times (R + r) + 2R$$

therefore the predation boundary (convex) is

$$\min((PI \times (R + r) + 2R), (s/r \times (R + r) + 2R))$$

which is a maximum when

$$PI \times (R + r) + 2R = s/r \times (R + r) + 2R$$

whence $r' = s/PI$ (or alternatively s (step) = circumference/2)

Predator avoidance

Predator avoidance by squirrelling about the perch and interposing the stem between the larva and the potential predator will also require a preferred stem radius $r' = s/PI$.

Utility

All three mechanisms postulated: predator avoidance; prey attack within an area; prey attack around a boundary; predict that the preferred stem radius should be the lateral steplength/PI (that is the animal is able to get halfway around the stem in one step – which seems reasonable enough).

To distinguish between the postulated perch uses it is necessary to examine the effects of varying perch radius from the preferred size established above. Two effects can occur: either perch utility is reduced more gently for perch sizes smaller than that preferred than for oversized perches or else perch utility reduces more drastically for perches smaller than the preferred size than for oversized perches.

It is immediately apparent that predator avoidance requires a perch at least as large as the preferred size and hence has the second type of response surface.

For prey attack over an area with $r < r'$

$$dA = - \pi \times R \ dr$$

For prey attack over an area with $r > r'$

$$dA = - s \times (R^2/(2r^2)) \ dr$$

$$dA)_{r'} = - s \times (R^2 \pi^2/(2s^2)) \ dr$$

$$dA)_{r'} = - R^2 \pi^2/(2s) \ dr$$

which for $s < \pi \times R/2$ has the first type of response. Smaller radius perches should be preferred to oversized perches.

For prey attack on a boundary when $r < r'$

$$dC = - \pi \ dr$$

For prey attack on a boundary when $r > r'$

$$dC = - s \times (R/r^2) \ dr$$

$$dC)_{r'} = - \pi^2 R/s \ dr$$

which for $s < \pi \times R$ again has the first type of response. Smaller radius perches should be preferred to oversized perches.

Thus for small changes from the preferred radius and biologically reasonable values of s both predation models predict a greater utility is realised by choosing perches of smaller radius, in contrast the predator avoidance model predicts a greater utility from the selection of oversized perches.

Tests of stem preference (Chapter 8) indicate an indifference to oversized stems but a general rejection of undersized stems. This is consistent with a predator avoidance strategy, but not with a strategy which maximises prey attack opportunity.

APPENDIX 4

The position of each larva in each aquarium was recorded daily at noon. In addition short term (hourly or two hourly scans) were made for 24 - 48h at a time at irregular intervals. This dataset was transferred to microcomputer and the information of interest abstracted. Three such abstractions are presented here.

Key to site types

- A - 8 'trees' + 3 roots B - 4 stems+4trees+3roots C - 4 x 5mm+4x2mm stems
- A1 -8 'trees' B1 - 8x5mm stems
- A2 -8 'trees' + 'leaves' B12- 8x5mm stems+3 roots
- B2- 8x 2mm stems
- B3 - 8x7mm stems

Key to distribution

Distribution data for each aquarium is presented in the form x(y, z) where x represents the position, y the larvae facing down (or out on roots or branches), z the larvae facing up (or in on roots and branches). The position information was coded: 0 = (0-3), 1 = (3-6), 2 = (6-9), 3 = (9-12) cm from base of stem; 4, 5 and 6 are the bottom, middle and top branches and 9 codes for roots on the floor.

Behaviour of solitary larvae on perches with Simocephalus as food

ID.	setup	distribution
1	A	0(56,7); 1(10,11); 2(2,23); 4(2,0); 5(1,1); 9(12,2)
2	A	0(37,7); 1(6,4); 2(3,4); 4(2,1); 5(5,2); 9(10,4)
3	B	0(97,20); 1(12,11); 2(10,68); 4(6,3); 5(9,5); 9(37,44)
7	C	0(14,1); 1(4,1)
11	A1	0(12,1); 1(3,0); 2(0,2)
20	A2	0(2,10); 1(1,0); 3(1,4); 4(0,1); 5(3,2)
21	A2	2(1,1); 3(0,11); 4(5,1); 5(7,4)
22	A1	0(57,8); 1(5,1); 2(7,6); 3(2,36); 4(5,3); 5(2,2)
23	A2	0(1,0); 3(0,13); 5(8,2)
33	A1	0(65,7); 1(8,1); 2(8,6); 3(3,15); 4(2,0); 5(0,2); 6(0,2)
34	B2	0(85,4); 1(10,10); 2(10,6); 3(3,24)

Behaviour of solitary larvae on perches with Daphnia as food

ID.	setup	distribution
4	B	0(69,4); 1(6,6); 2(2,5); 4(6,15); 5(1,0); 9(15,9)
5	B	0(119,3); 1(21,16); 2(5,4); 3(0,2); 4(19,26); 5(7,2); 9(15,18)
13	A1	0(33,6); 1(9,4); 2(4,16); 4(1,2); 5(0,2)
15	B12	0(49,6); 1(5,3); 2(1,0); 9(25,18)
16	B12	0(12,2); 9(1,5)
17	B12	0(8,0); 1(2,0); 2(0,2); 9(3,3)
25	A2	0(15,1); 1(3,2); 2(7,5); 3(1,19); 4(2,0); 5(2,4); 6(17,7)
27	B3	0(60,1); 1(1,2); 2(10,4); 3(8,22)
36	B1	0(7,0); 1(2,0); 2(0,4); 3(2,6)

Behaviour of solitary larvae on perches with Opifex as food

ID.	setup	distribution
6	A	0(16,1); 1(11,2); 2(2,0); 9(2,9)
8	B1	0(119,14); 1(27,17); 2(16,9); 9(29,55)
10	C	0(32,9); 1(8,6); 2(1,4)
	A1	0(84,11); 1(33,15); 2(7,8); 4(3,1)
18	B12	0(221,5); 1(11,6); 2(4,3); 9(3,2)

Behaviour of solitary larvae on perches with Lumbriculus as food

ID.	setup	distribution
28	A1	0(46,8); 1(20,7); 2(18,6); 3(5,12); 4(0,1); 5(1,0)
29	B2	0(22,0); 1(7,1); 2(24,14); 3(5,17)
30	B2	0(29,3); 1(12,3); 2(11,30); 3(3,10)
32	A1	0(90,22); 1(17,11); 2(21,5); 3(0,21); 4(2,0); 5(0,2); 6(1,0)
37	B1	0(14,6); 1(5,5); 2(5,2)
38	B1	0(33,3); 1(11,2); 2(21,6); 3(5,5)
39	A1	0(38,15); 1(25,25); 2(5,13); 3(0,1); 5(4,2); 6(5,1)
40	B1	0(15,2); 1(4,3); 2(4,0); 3(11,9)
41	B1	0(33,2); 1(8,5); 2(14,5); 3(22,30)
42	B1	0(32,3); 1(9,3); 2(8,2); 3(12,22)

Behaviour of solitary larvae on perches without food

ID.	setup	distribution
19	A1	0(48,4); 1(1,3); 2(16,7); 3(1,9); 4(1,4)
26	B2	0(50,3); 1(0,3); 2(9,3); 3(7,6)
31	A2	0(57,1); 1(4,1); 2(14,14); 3(1,16); 4(8,4); 5(2,0); 6(0,1)

Distribution of larvae on sites with more than one occupant. T1/T0 is the total site occupations recorded over the total possible number of site occupations.

Behaviour of larvae on multiply occupied perches with Simocephalus as food

ID.	setup	distribution	T1 / T0
1	A	0(8,2); 1(0,1); 2(0,5); 4(1,2); 5(0,0); 9(8,6)	187/190
2	A	0(12,2); 1(5,2); 2(1,4); 3(0,1); 4(2,0); 5(2,0); 6(1,0); 9(0,1)	124/130
3	B	0(16,4); 1(1,1); 2(6,9); 4(5,1); 5(4,2); 9(15,13)	404/452
7	C	0(3,1); 1(1,0); 2(1,0); 4(1,0); 5(1,0)	28/32
11	A1	0(1,2); 1(1,0)	22/32
12	A1	0(13,4); 1(7,1); 2(4,7); 4(2,0); 5(1,0)	224/275
20	A2	0(4,1); 3(2,1); 4(1,2); 5(2,4)	31/40
21	A2	0(1,0); 3(0,5); 4(1,0); 5(7,6)	60/74
22	A1	0(12,2); 1(1,1); 2(2,2); 3(1,9); 4(3,1); 5(0,2)	174/228
23	A2	3(0,2); 5(2,4)	33/54

Behaviour of larvae on multiply occupied perches with Daphnia as food

4	B	0(6,0); 1(2,0); 2(0,4)	150/152
5	B	0(12,1); 1(5,0); 2(1,4); 4(2,2); 5(1,0); 6(1,0); 9(1,3)	356/409
13	A1	0(10,5); 1(2,3); 2(1,5); 4(1,0)	105/127
15	B12	0(4,2); 2(2,1); 4(0,1); 5(1,1); 9(4,11)	141/145
16	B12	0(1,0); 1(1,0); 9(1,1)	24/32
17	B12	0(6,4); 1(2,2); 2(0,3); 5(0,1); 9(6,7)	48/48

Behaviour of larvae on multiply occupied perches with Opifex as food

6	A	0(3,0); 1(2,0); 5(1,0)	49/56
8	B1	0(2,0); 1(2,0); 2(3,0); 9(8,12)	342/397
10	C	0(11,2); 1(10,3); 2(0,1); 4(2,0); 5(1,3)	114/120
14	A	0(2,1); 9(2,0)	72/129
18	B12	0(10,0); 1(0,1); 2(0,8)	302/303

Behaviour of larvae on multiply occupied perches without food

19	A1	0(4,1); 1(1,0); 2(2,1); 3(0,1); 4(5,1)	112/124
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Durations of site occupation by individual X. zealandica larvae.

Durations in days, - indicates not on any site.

Aquarium 1.

larva

1. 1, 6, 1, 3, 1, 8, 6, 1, 1
2. 2, 1, 3, 1, 1, 2, 2, 2, 1, 1, 1, 8, 1, 2
3. 1, 1, 1, 1, 2, 2, 1, 4, 11, 1, 1, 1
4. 1, 3, 1, 1, 1, 1, 13, 1, 2, 2, 1, 1
5. 4, 4, 1, 1, 2, 2, 2, 2, 5, 1, 1, 1
6. 4, 2, 7, 11, 1, 2
7. 1, 2, 1, 8, 2, 6, died
8. 4, died

Aquarium 8

1. 1, 37
2. 1, 1, 1, 2, 2, 2, 2, 17, 3, 6, 1, 18
3. 1, 2, -, 1, emerged
- 3a. 1, 6, 1, 1, -, 1, 7, 2, 1
4. 1, 1, 7, -, emerged
- 4a. 2, 25, 4
5. 1, 1, 1, 5, 37
6. 1, 1, 24, - (20 days)
7. 1, 10, 45
8. 1, 1, 42, 12